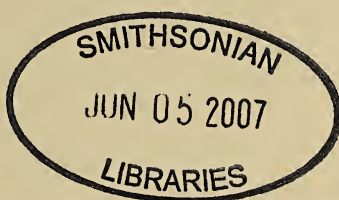


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The Journal of ARACHNOLOGY

OFFICIAL ORGAN OF THE AMERICAN ARACHNOLOGICAL SOCIETY



VOLUME 35

2007

NUMBER 1

THE JOURNAL OF ARACHNOLOGY

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The Journal of Arachnology (ISSN 0161-8202), a publication devoted to the study of Arachnida, is published three times each year by *The American Arachnological Society*. **Memberships (yearly):** Membership is open to all those interested in Arachnida. Subscriptions to *The Journal of Arachnology* and *American Arachnology* (the newsletter), and annual meeting notices, are included with membership in the Society. Regular, \$40; Students, \$25; Institutional, \$125. Inquiries should be directed to the Membership Secretary (see below). **Back Issues:** Patricia Miller, P.O. Box 5354, Northwest Mississippi Community College, Senatobia, Mississippi 38668 USA. Telephone: (601) 562-3382. **Undelivered Issues:** Allen Press, Inc., 810 E. 10th Street, P.O. Box 368, Lawrence, Kansas 66044 USA.

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Cover photo: Web of female bowl and doily weaver *Frontinella communis* (Araneae, Linyphiidae) suspended in *Palafoxia feayi* (Asteraceae) in Florida scrub habitat. Photo by Jim Carrel.

Publication date: 22 May 2007

Ⓒ This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).

SUBADULT FEMALE EXPERIENCE DOES NOT INFLUENCE SPECIES RECOGNITION IN THE WOLF SPIDER *SCHIZOCOSA UETZI* STRATTON 1997

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ABSTRACT. In many vertebrate systems, early experience has been linked to the learning of species-specific traits that are subsequently assessed during mate choice, thus ensuring conspecific matings. In invertebrate systems, however, early experience was not thought to play a role in mate choice until a recent study using *Schizocosa uetzi* Stratton 1997 wolf spiders demonstrated that females mate more readily with males of a familiar versus unfamiliar phenotype. The function of early mate choice learning in this system is not yet known, but a role in learning species-specific traits seems unlikely. In northwestern Mississippi, *S. uetzi* is found sympatrically with *S. stridulans* Stratton 1991, which matures slightly earlier in the season. If *S. uetzi* early mate choice learning functions in learning species-specific traits used in mate choice, as is often the case in vertebrate systems, then subadult female exposure to heterospecifics (*S. stridulans*) could result in heterospecific matings. Here, I exposed subadult *S. uetzi* females to courtship advances from mature males of either *S. uetzi* (conspecifics) or *S. stridulans* (heterospecifics) in order to test a species-specific mate choice learning function. Previously exposed females were paired with a mature male of the same, or the opposite, species as their exposure male. As expected, the results do not support a species-specific mate choice learning function. Previously exposed females mated significantly more with conspecific males regardless of their exposure treatment, as did unexposed females. The highest pre-mating sexual cannibalism rates occurred in heterospecific mate choice trials regardless of the exposure treatment, and exposed females were more likely to cannibalize males than unexposed females. While previous results demonstrate that subadult experience influences conspecific mate choice, a species recognition template seems to exist that is independent of the influence of early experience. The potential influence of multimodal signal interactions on conspecific mate choice learning is discussed.

Keywords: Experience, Araneae, Lycosidae, species recognition, mate choice, cannibalism

Conspecific mating preferences have traditionally been thought to be under genetic control (sensu Fisher 1958). However, considerable evidence has been building, suggesting the importance of environmentally and socially influenced mating preferences (for reviews see Dugatkin 1996a; Brooks 1998; Irwin & Price 1999; Owens et al. 1999; Freeberg 2000; White 2004). For example, predation risk has been shown to alter female guppy preferences for male traits (Gong & Gibson 1996). Female satin bower birds of different ages utilize different criteria in choosing males (Coleman et al. 2004). Female guppies and Japanese quail alter their mate choice decisions based on the mate choice of other females (Dugatkin 1992a, 1992b, 1996b; Galef & White 2000; White & Galef 2000; White 2004). Sexual imprinting has even been suggested to be the rule rather than the exception for the origin of mating preferences in birds (ten Cate 1993).

While virtually all of the examples involving the influence of early experience on subsequent mate choice have traditionally involved vertebrates, a recent study provides one of the first examples of socially influenced mating preferences in an invertebrate. After exposure to mature males as subadults, adult female wolf spiders (*Schizocosa uetzi* Stratton 1997) were shown to mate significantly more with males of a familiar versus unfamiliar phenotype (Hebets 2003). Furthermore, as adults, these exposed females were more likely to cannibalize males of an unfamiliar phenotype (Hebets 2003). Due to the potential for sexual cannibalism in this system, the selection pressure placed on mating behavior is extremely high. As such, social interactions that influence the origin or maintenance of female mating preferences could potentially play an important role in the subsequent evolution of male secondary sexual traits.

The finding that the adult mate choice of *S. uetzi* females is dependent on subadult female experience is not only important because it expands the probable importance of socially influenced mate choice to include non-vertebrate groups, but it also represents a life stage (subadult females) during which mate choice learning has not been frequently explored. Most studies of mate choice learning focus on either a period very early in life or on experiences females have as adults. Sexual imprinting, for example, is typically restricted to a critical period early in life and is frequently argued to be a means by which young birds learn species-specific characteristics (Bateson 1966; Immelmann 1975; Irwin & Price 1999). In contrast, mate choice copying, or imitation, involves already mature females copying the mate choice of other mature females and is often thought of as a means of avoiding costs associated with mate choice (i.e., search time and costs of assessing mates) (see review White 2004). If sexual imprinting functions to insure conspecific adult mate choice, it follows that the influences are limited to a critical period early in life in taxa with parental care; both factors that increase the likelihood that an individual will imprint on its parents. In the case of mate choice copying, as an adult that is putatively ready to mate, imitating the choices of others is also logical as it could potentially cut down on costs and time associated with choosing a mate independently. However, in the case of the wolf spider *S. uetzi*, exposure experiments demonstrated an effect of subadult experience on adult mate choice. This experience was gained during a female's penultimate life stage. Due to the short lifespan of these spiders (~1 yr) and the lack of parental care, it is impossible for subadult females in the field to gain experience with parental phenotypes. Furthermore, an effect of experience was demonstrated before females were mature, hence, prior to their ability to mate, thus ruling out mate choice copying. The question then arises regarding the potential influence and/or function of subadult mate choice learning on subsequent adult mate choice in natural populations of the wolf spider *S. uetzi*.

While innate recognition of species specific language and song has certainly been demonstrated, early experience with siblings or parents in many species is crucial for learning

species-specific characteristics (Laland 1994; Irwin & Price 1999; ten Cate & Vos 1999). In several studies involving cross-fostering experiments with birds as well as mammals, sexual imprinting has been shown to lead to heterospecific mate choice (Kendrick et al. 1998; Penn & Potts 1998; Slagsvold et al. 2002). Examples involving early learning of species-specific characteristics tend to involve species with parental care. Based on the lack of parental care in wolf spiders as well as the high degree of sympatry among *Schizocosa* species in the southeast (personal observation), it seems unlikely that subadult female mate choice learning in *S. uetzi* functions to insure specific-specific adult mate choice. Since species recognition requires that only one signal variant be recognized by all members of one species, species recognition mechanisms are often hard-wired (Bradbury & Vehrencamp 1998). Previous studies exploring other wolf spider species, including members of the genus *Schizocosa*, demonstrate a lack of hybridization between closely related species (Stratton & Uetz 1981, 1986; Stratton 1983; Costa & Francescoli 1991). However, forced copulations between closely related species produced viable offspring, suggesting a low cost for heterospecific matings (Stratton & Uetz 1981). Regardless, prior heterospecific mate choice studies of spiders involved naïve, inexperienced females. The potential for subadult female experience to influence species-specific mate choice recognition has not yet been examined in spiders and before other hypotheses regarding the function of subadult female mate choice learning in *S. uetzi* can be explored, one must rule out the possibility of species-specific mate choice learning.

Schizocosa uetzi overlaps, at least partially in time and space, with several other species of *Schizocosa*, most notably *S. stridulans* Stratton 1991 (pers. obs.) with which it is closely related (Stratton 1991, 1997, 2005; Vink & Hebets unpublished data). Laboratory studies using *S. uetzi* and *S. stridulans* individuals suggest that females of each species will occasionally display receptively to heterospecific males under conditions where the background levels of noise in both the visual and seismic signaling environments are manipulated (Hebets unpublished data). Furthermore, the male courtship behavior and morphology of *S. uetzi* and *S. stridulans* is very

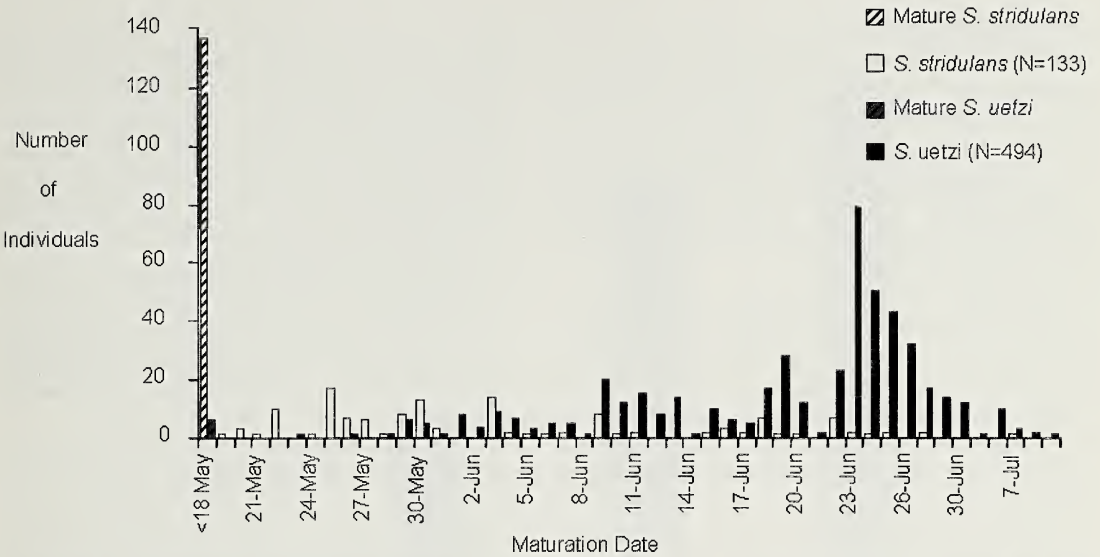


Figure 1.—Maturation dates (three seasons) for *S. stridulans* and *S. uetzi* (2001–2003). Prior to the 19th of May, 137 *S. stridulans* and 6 *S. uetzi* were collected from the field already mature, indicating the slightly earlier maturation time of *S. stridulans*. All other data represent the dates of maturation in the laboratory. In all years, many already mature individuals were observed but not collected and, thus, this graph is a conservative estimate of species overlap.

similar and, without examination under a microscope, it is impossible to tell females of the two species apart. If subadult female mate choice learning functions to insure subsequent conspecific matings in *S. uetzi*, then the prevalence of heterospecific males (*S. stridulans*) in the system could result in adult mate choice “mistakes,” or misidentifications.

Here I explore the possibility that early experience provides an opportunity for subadult females to learn species-specific characteristics by examining the potential influence of subadult experience on heterospecific mate choice in the wolf spider *S. uetzi*. To test the hypothesis that early experience functions in species-specific mate choice learning, I exposed subadult *S. uetzi* females to either conspecific or heterospecific mature males. On their maturation, I then paired these previously exposed females with a mature male of either the same or the opposite exposure treatment for mate choice trials. As a control, a group of unexposed females were paired with conspecific or heterospecific mature males upon maturation.

METHODS

Species.—*Schizocosa uetzi* and *S. stridulans* are sister species (Vink & Hebets unpub-

lished data) found sympatrically in the deciduous forests of northwestern Mississippi, USA. They are similar in size and are often difficult to distinguish. A combination of 3 yr worth of collection data (2001–2003) reveals that while the peak maturation time for *S. stridulans* is in late May as compared to late June for *S. uetzi*, there is still significant overlap in maturation times and mature individuals of both species can be present simultaneously in the field (Fig. 1). Due to their morphological similarities as well as their potential overlap in both space and time, *S. stridulans* males were used as the heterospecific species in this experiment. Subadult *S. uetzi* and *S. stridulans* of both sexes were collected from sites near Oxford, Mississippi, USA in May 2003 and brought back to the laboratory where they were housed individually in 6 × 6 × 8 cm AMAC plastic products boxes. Individuals were fed 2–3 crickets once a week, were provided with a constant source of water, and were kept on a 12L:12D cycle. All cages had opaque sides to insure visual isolation. Spiders were checked at least every other day for molts and the maturation date for all individuals was recorded. On completion of all experiments, I examined preserved females un-

der a dissecting scope to insure species identity. I used ~15 known *S. stridulans* females and ~15 known *S. uetzi* females from prior laboratory matings (Hebets 2002) in order to establish the within-species variation in epigynal characters. Using known individuals of each species as a comparison, I determined the species identity of every female used in this experiment.

Exposure trials.—Subadult *S. uetzi* females were randomly assigned to either a conspecific (*S. uetzi*) or heterospecific (*S. stridulans*) male treatment. During their penultimate stage, subadult females were placed in an arena with a mature male of their assigned treatment for 30 min every other day until their final maturation molts. Females were never exposed to the same male twice. All experimental arenas were $8.73 \times 8.73 \times 11.27$ cm Amac Plastic Product clear boxes and had a single piece of filter paper lining the bottom. The night prior to both exposure trials and mate choice trials, a mature *S. uetzi* female was placed on the filter paper and left overnight. Mature females deposit silk along with an associated pheromone that will elicit courtship behavior in mature males even in the absence of a female. Once courtship is elicited, males will direct their courtship towards any spider present, providing the subadult females with experience with either conspecific or heterospecific courting adult males. Only two *S. stridulans* males were used twice during the exposure trials, but not with the same female, and all other males were used only once (*S. stridulans*, $n = 29$; *S. uetzi*, $n = 33$).

Mate choice trials.—Once the exposed females molted to maturity, they remained isolated in their individual cages until the mate choice trials. Mate choice trials of exposed females were conducted 11–20 d (= days) after their final maturation molts since mature females are not receptive immediately after maturation. In adult mate choice trials, females were randomly assigned either to males from the same treatment type as their exposure trials, or the opposite treatment type. Each female was paired with only one test male, resulting in four treatments: heterospecific exposure/heterospecific mate choice; heterospecific exposure/conspecific mate choice; conspecific exposure/heterospecific mate choice; and conspecific exposure/conspecific mate choice. Females were placed in the same

arenas as were used for the exposure trials and after 2 min of acclimation time, a male was introduced. All arenas were swabbed with alcohol in between trials. Mate choice trials lasted 30 min and trials were scored for the presence/absence of copulation, the latency to copulation (duration of time from beginning of trial until the male mount), and the presence/absence of sexual cannibalism. A total of 16 unexposed *S. stridulans* males were used, with two individuals used twice, and a total of 18 unexposed *S. uetzi* males were used only once each. Males were randomly assigned to trials.

Unexposed females.—The mate choice of unexposed females was also assessed in this study. Thirty-six subadult *S. uetzi* females were collected from the field and were placed in individual cages where they remained isolated until at least 11 d after their final maturation molts. These unexposed females were randomly assigned either a heterospecific or conspecific male treatment and were subjected to mate choice trials in the same manner as were the exposed females. Each unexposed female was only used once with one male. Voucher specimens are deposited in the University of Nebraska State Museum, Lincoln, Nebraska, USA.

RESULTS

Sixty-four subadult *S. uetzi* females gained experience with either heterospecific or conspecific mature males. Mating frequency was dependent on the treatment ($X^2 = 23.46$, $P < 0.001$, $df = 3$, Fig. 2). Exposed females mated significantly more with conspecific males versus heterospecific males ($X^2 = 10.85$, $P = 0.001$, $df = 1$, Fig. 2), but the type of male a female was exposed to did not influence mating frequency ($X^2 = 2.23$, $df = 1$, ns). This analysis includes all females.

While the courtship behavior of *S. uetzi* and *S. stridulans* males differ, their courtship effort was similar (*S. stridulans* 84% courted, *S. uetzi* 91% courted; $X^2 = 0.73$, ns). When I only analyzed the females for which males were known to engage in courtship during the exposure trials, the results were similar to analyses including all females ($X^2 = 21.93$, $P < 0.0001$, $df = 3$; *S. stridulans*/*S. stridulans* $n = 16$, 0% mated; *S. stridulans*/*S. uetzi* $n = 17$, 53% mated; *S. uetzi*/*S. stridulans* $n = 13$, 23% mated; *S. uetzi*/*S. uetzi* $n = 16$, 63%

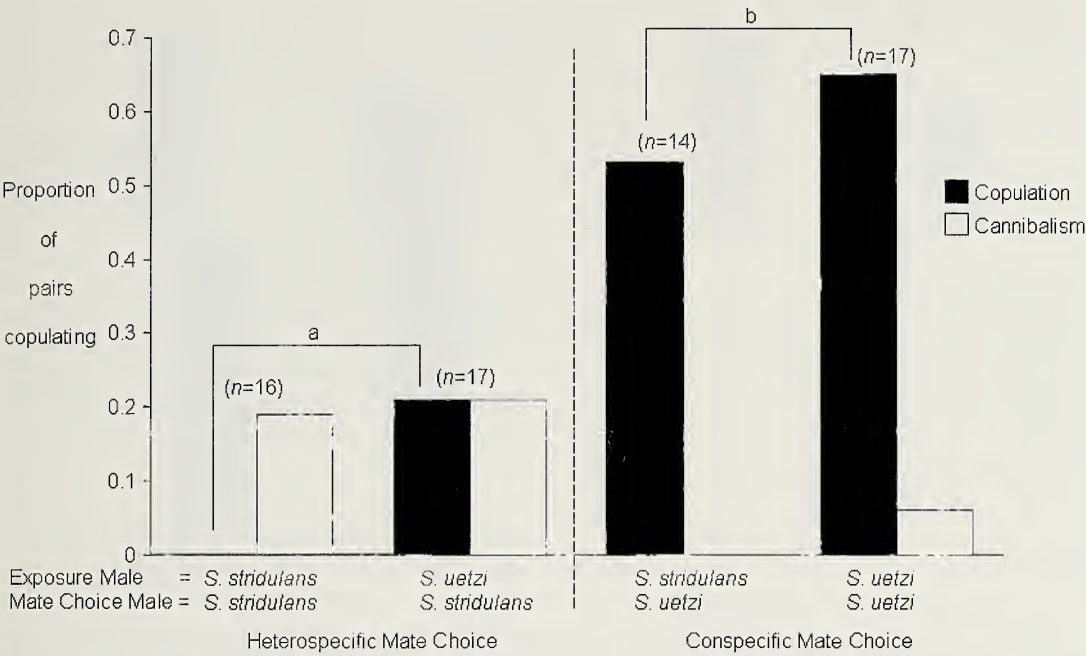


Figure 2.—Responses of female *S. uetzi* as measured by proportion of pairs copulating or proportion of pairs ending in cannibalism. Female *S. uetzi* were exposed as subadults to either heterospecific males (*S. stridulans*) or conspecific males (*S. uetzi*). As adults, these females were paired with either the same, or the opposite, male type as their prior exposure (heterospecific vs conspecific male) and were given an opportunity to mate. Mating frequency was dependent on treatment and pairs mated more frequently in conspecific mate choice trials versus heterospecific mate choice trials, regardless of the exposure treatment. Different letters indicate significant differences.

mated). Cannibalism frequency did not depend on the treatment regardless of whether all females are included ($X^2 = 6.6$, $df = 3$, ns), or when only females that were known to have been exposed to male courtship during the exposure trials were analyzed ($X^2 = 5.34$, $df = 3$, ns).

Sixty-one percent of the subadult females were exposed to more than one courting male. The maximum number of times a female was exposed was six. The number of times a female was exposed was independent of treatment ($F_{3,61} = 1.04$, ns; *S. stridulans*/*S. stridulans* mean \pm SE = 2.13 ± 0.34 ; *S. stridulans*/*S. uetzi* mean \pm SE = 2.41 ± 0.33 ; *S. uetzi*/*S. stridulans* mean \pm SE = 1.93 ± 0.36 ; *S. uetzi*/*S. uetzi* mean \pm SE = 1.94 ± 0.33). The number of times a female was exposed did not influence her likelihood to copulate ($F_{5,42} = 1.37$, ns; treatment: $F_3 = 1.04$, $P = 0.36$; copulate: $F_1 = 0.009$, $P = 0.92$; treatment \times copulate: $F_3 = 2.41$, $P = 0.10$), or her likelihood to cannibalize ($F_{5,41} = 1.42$, ns; treatment: $F_3 = 0.48$, ns; cannibalize: F_1

= 0.55 , $P = 0.58$; treatment \times copulate: $F_3 = 1.87$, ns).

Unexposed females mated significantly more with conspecific males than with heterospecific males (conspecific males $n = 18$, 39% copulated; heterospecific males $n = 18$, 11% mated; $X^2 = 3.87$, $P = 0.049$, see Fig. 3), and there were no cannibalism events with unexposed females. The latency to copulation did not differ among any of the treatments in which copulation occurred ($F_{4,27} = 0.39$, ns; *S. stridulans*/*S. uetzi* $n = 9$, mean \pm SE = 9.88 ± 2.5 ; *S. uetzi*/*S. stridulans* $n = 3$, mean \pm SE = 10.59 ± 4.3 ; *S. uetzi*/*S. uetzi* $n = 11$, mean \pm SE = 10.10 ± 2.3 ; unexposed/*S. stridulans* $n = 2$, mean \pm SE = 12.47 ± 5.3 ; unexposed/*S. uetzi* $n = 7$, mean \pm SE = 6.58 ± 2.8).

When exposed and unexposed trials are combined, mating frequency is dependent on treatment ($X^2 = 28.63$, $P < 0.0001$) with mating frequencies significantly higher when the treatments involve *S. uetzi* as the mate choice male (i.e., a conspecific) as opposed to *S. stri-*

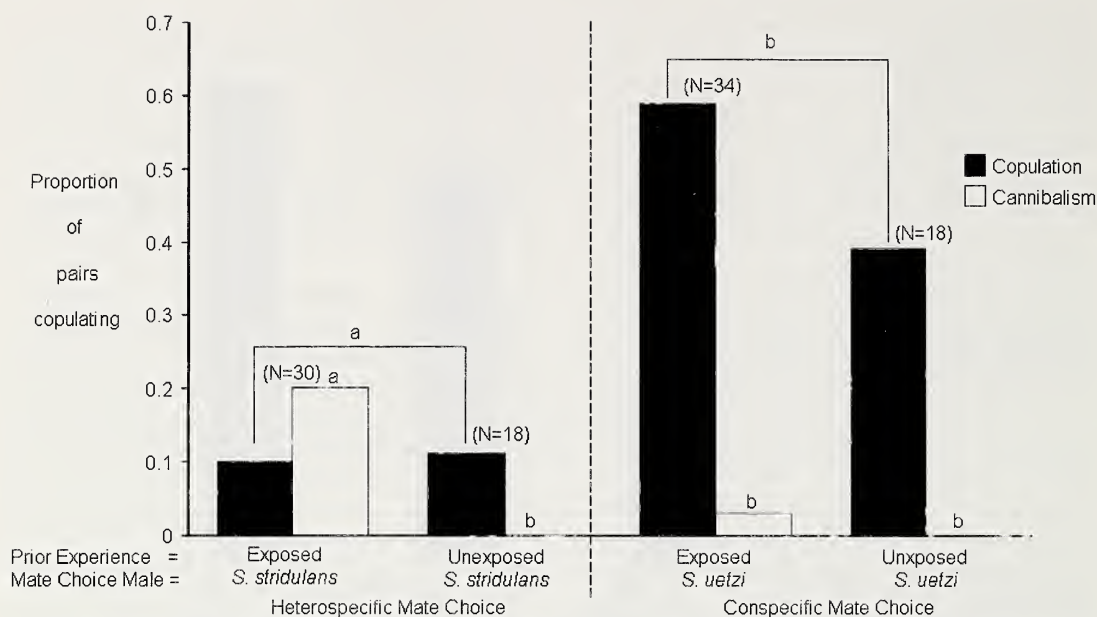


Figure 3.—*Schizocosa uetzi* female responses as measured by proportion of pairs copulating or proportion of pairs ending in cannibalism. *Schizocosa uetzi* females were either exposed to a mature male as a subadult (includes all exposures regardless of male type) or were unexposed (no known prior exposure to any mature male). As adults, females were paired with either a heterospecific male (*S. stridulans*) or a conspecific male (*S. uetzi*) and were given an opportunity to mate. Regardless of whether females were exposed or not, they mated significantly more with conspecific males than heterospecific males. Cannibalism rates were significantly higher with previously exposed females paired with heterospecific mate choice males compared to all other categories.

dulans (i.e., a heterospecific). An analysis that ignores the exposure males and lumps all similar mate choice trials together results in this same pattern: mating frequency is significantly higher with conspecific versus heterospecific mate choice trials ($X^2 = 23.18$, $P < 0.0001$, Fig. 3). Precopulatory cannibalism rate is also dependent on treatment with exposed females paired with *S. stridulans* (heterospecific) having higher cannibalism rates than any other treatment category ($X^2 = 11.68$, $P = 0.009$; Fig. 3).

In a comparison that combined all exposed females versus unexposed females, mating frequency does not depend on the presence/absence of exposure ($X^2 = 1.3$, ns, Fig. 4). However, cannibalism frequency does depend on the presence/absence of exposure, with more cannibalisms occurring with the exposed females versus the unexposed females ($X^2 = 6.5$, $P = 0.01$, Fig. 4). When comparing only the subset of females that were exposed to *S. uetzi* males and paired with *S. uetzi* males for mate choice trials (*S. uetzi*/*S. uetzi*) to unex-

posed females paired with *S. uetzi* males, there is no statistical difference between exposed and unexposed females with respect to copulation frequency ($X^2 = 2.4$, ns, $P = 0.12$, Fig. 5).

DISCUSSION

While several studies involving both birds and mammals have demonstrated that early experience with heterospecifics can lead to heterospecific mating preferences later in life (Kendrick et al. 1998; Penn & Potts 1998; Slagsvold et al. 2002), this same effect is not seen in *S. uetzi* wolf spiders. Here, I confirm the expectation that a subadult female's experience with only heterospecific males does not lead to heterospecific mate choice preferences. Even when exposed to heterospecific males as subadults, *S. uetzi* females preferred to mate with conspecific males. This preference for conspecific males was present in both exposed as well as unexposed females. These results suggest that a strong species recognition template is in place for *S. uetzi* and that

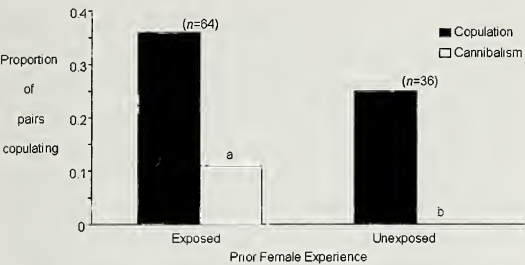


Figure 4.—The effect of exposure on the likelihood of *S. uetzi* females to copulate and cannibalize. Exposed females tend to copulate more frequently than unexposed females, although this is not significant. Exposed females are however, more likely to cannibalize a male than unexposed females.



Figure 5.—The effect of exposure on the likelihood of *S. uetzi* females to mate with or to cannibalize conspecific males, comparing those previously exposed to a conspecific male vs those with no prior experience with any mature male (exposure/mate choice = *S. uetzi*/*S. uetzi* vs unexposed/*S. uetzi*). Exposed females tend to mate more frequently than unexposed females, but the difference is not significant.

subadult female mate choice learning does not function to insure subsequent conspecific recognition.

Nevertheless, while females significantly preferred conspecific males, five of the females tested did mate with heterospecific, *S. stridulans* males. Unfortunately, the species identity of these five individuals could not be confirmed. *Schizocosa stridulans* and *S. uetzi* are extremely similar and it is particularly difficult to tell females apart and virtually impossible without examining their genitalia. Unfortunately, the preserved bodies of these females could not be located. Thus, without a close examination of these five females, I cannot be certain that they were not *S. stridulans* females and thus cannot confirm the existence of any heterospecific matings between these two species. The species identity of all other females was confirmed by examining their genitalia under a dissecting scope.

While exposure itself did not significantly influence mating frequency, Figures 4 and 5 illustrate a compelling trend suggesting that exposed females are more likely to mate than unexposed females. This same trend, suggesting that experience leads to an increased likelihood to mate, was also demonstrated in the original study exploring the influence of early experience on adult mate choice in *S. uetzi* (Hebets 2003). The potential influence of early experience on the likelihood to mate is certainly intriguing and I believe that future studies that control for female age across treatments and involve larger samples sizes of unexposed females will be successful in further illuminating this pattern.

Although exposure itself did not significantly influence mating frequency, it did influence cannibalism frequency. Compared to unexposed females, females that were exposed to courtship advances from mature males as subadults were more likely to cannibalize males in subsequent adult encounters. Specifically, exposed females were more likely to cannibalize heterospecific males, regardless of their exposure treatment. Exposed females were more likely to cannibalize males than unexposed females in the Hebets (2003) study as well ($\chi^2 = 5.55, P = 0.02$). Interestingly, in both Hebets (2003) and the present study, unexposed females never engaged in pre-copulatory sexual cannibalism. In both studies, since females were collected from the field as early penultimates, the mate choice trials may have represented the first time that these unexposed females experienced courtship advances from mature males, and therefore, represented the first time females acquired knowledge of the presence of mature males. This knowledge, or lack thereof, regarding the existence of other males may influence a female's readiness to cannibalize. Unexposed females may have a higher perceived cost associated with a missed detection (sensu Wiley 1994), or misidentification, than exposed females, and thus may be more cautious in their distinction between conspecific versus heterospecific males (or between mate and meal). Examining the influence of experience on a female's perceived costs and ben-

efits of mate choice/cannibalism represents an intriguing direction for future research.

Until now, the two most common functions of the influence of early experience on subsequent mate choice have involved (1) insuring conspecific mate choice (often via sexual imprinting) or (2) reducing the costs associated with searching and assessing potential mates (via mate-choice copying). This study suggests that neither function is generally applicable to the subadult mate choice learning of *S. uetzi*. However, the learning of species-specific visual characteristics remains a possibility. Results from Hebets (2003) suggest that subadult female *S. uetzi* specifically learn visual characteristics of conspecific mature males, which are subsequently used in adult mate choice decisions (i.e., visual learning). While the previous study involved experimentally manipulating visual secondary sexual traits of males and subsequently assessing female mate choice, it did not rigidly control for effects of odor learning (Hebets 2003). Nonetheless, since spiders are not known to possess sensory structures characteristic of olfactory perception (Foelix 1996), and since mate choice happens before any male-female contact that could lead to the potential perception of contact chemicals, visual learning remains the most plausible explanation. However, *S. uetzi* males, along with many other species in the genus, use seismic signals in addition to visual signals in their courtship displays (multimodal signaling: Rovner 1975; Stratton & Uetz 1981, 1983; Stratton & Uetz 1983; Barth 1986; Hebets & Uetz 1999; Uetz & Roberts 2002; Hebets 2005). The seismic signals appear to be species specific (Stratton & Uetz 1981; Elias & Hebets unpublished data) and are thought to be ancestral in this genus. Previous work assessing the function of multimodal signaling in *S. uetzi* has already demonstrated that the visual and seismic signals interact such that females respond differently to varying visual signals only in the presence of a seismic signal (Hebets 2005). Thus, the seismic signal appears to focus a female's attention on the visual signal.

In light of the attention-altering hypothesis of multimodal signaling in *S. uetzi*, results of the present study are consistent with the notion that the seismic signal of *S. uetzi* male courtship may function as a password for species recognition (sensu Hauber et al. 2001).

Females may learn conspecific visual male traits only in the presence of a conspecific seismic courtship signal. Since all of the exposure trials included seismic signals, females may have only engaged in subadult mate choice learning of visual signals in the presence of a conspecific seismic signal, which meant learning only the visual morphology of a conspecific male. Experiments involving seismic exposure to conspecific male courtship signals simultaneous with visual exposure to heterospecific male courtship signals would further elucidate this possibility. Cross-modal signal interactions influencing learning have already been demonstrated in several taxa. For example, the presence of sound has been shown to significantly increase the speed with which chicks can learn to avoid unrewarding visual stimuli (Rowe 2002). A whistle has been shown to serve as a cue for song learning in the white-crowned sparrow (Soha & Marler 2000). In a similar fashion, the presence of a conspecific seismic signal may facilitate a subadult female's learning of visual characteristics in *S. uetzi*.

In summary, this study demonstrates that subadult female experience does not influence general adult species-specific mate recognition in the wolf spider *S. uetzi*. Instead, results suggest that there is a species recognition template in place that is independent of the effect of early experience. This species recognition template likely involves the seismic courtship signal. In conclusion, a potential adaptive value associated with subadult female learning remains unknown, but, if found, it will likely prove to be novel among the known functions of social influences of mate choice.

ACKNOWLEDGMENTS

I would like to thank G. Stratton and P. Miller for help in collecting spiders and in providing food, lodging, and insightful conversations during collecting trips. K. Cuasay and D. Nee helped in exposure as well as mate choice trials. D. Elias, D. Papaj, R. Hoy, N. VanderSal, K. Fowler-Finn, A. Spence, and J. Storz all provided useful comments and suggestions. The work was conducted in the lab of R. Hoy and was funded by an NIH training grant to the Department of Neurobiology and Behavior, Cornell University, Ithaca, New York.

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Manuscript received 11 October 2005, revised 9 August 2006.

FREE-LIVING SPIDERS OF THE GENUS *ARIAMNES* (ARANEAE, THERIDIIDAE) IN HAWAII

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ABSTRACT. This study examines species in a relatively diverse lineage of *Ariamnes* spiders in the Hawaiian archipelago, where they appear to have undergone adaptive radiation, with several species generally co-occurring at any one locality. The lineage was initially described by the single species *A. corniger* Simon 1900. The Hawaiian representatives of this lineage are characterized by variably elongate abdomens and are mostly free-living, at least as adults, although a number have been found to occur, at least facultatively, as kleptoparasites on the webs of other spiders. These spiders are all nocturnal. Their phylogenetic affinities with other representatives of the genus outside the Hawaiian Islands are unclear. Ten new species are described here: *A. kahili*, *A. huinakolu*, *A. makue*, *A. uwepa*, *A. poele*, *A. melekalikimaka*, *A. alepeleke*, *A. laau*, *A. waikula*, and *A. hiwa*. These species, together with the single described species *Ariamnes corniger*, include all known representatives of the lineage in the Hawaiian Islands. Different species occur in middle and high elevations and in wet and dry habitats.

Keywords: Descriptions, new species, taxonomy, *Argyrodes*, islands, Pacific Ocean

The spider subfamily Argyrodinae (Theridiidae) comprises six genera, *Argyrodes* Simon 1864, *Faiditus* Keyserling 1884, *Neospintharus* Exline 1950, *Ariamnes* Thorell 1869, *Rhomphaea* L. Koch 1872, and *Spheropistha* Yaginuma 1957, the latter five genera having recently been removed from synonymy with *Argyrodes* (Agnarsson 2004). The original genus *Argyrodes* was considered to be distinct from two related genera, *Rhomphaea* and *Ariamnes*, based on differences in eye arrangement, clypeal modification, and relative length of metatarsi (Simon 1893). These characters were found not to separate groups reliably and so *Rhomphaea* and *Ariamnes*, together with *Faiditus*, *Neospintharus*, and *Spheropistha*, were incorporated into the composite genus *Argyrodes* (Exline & Levi 1962). However, a number of authors did not accept the synonymy of all of these genera, and *Ariamnes* and *Rhomphaea* (the two most distinct genera), in particular, continued to be used as generic descriptors (Forster & Forster 1999). Finally, arguing that the distinction between genera was quite clear-cut, Yoshida (2001) resurrected the genera *Rhomphaea*, *Ariamnes*, and *Spheropistha*. Moreover, recent work by Agnarsson (2004) also resurrected *Faiditus* and *Neospintharus* on the basis that all of

these genera are required to render the subfamily Argyrodinae monophyletic. The diversity represented by the current subfamily delimitation includes some of the most extraordinary behaviors known in spiders, in particular kleptoparasitism, a rather unusual form of species interaction in which one partner steals food from the other (Elgar 1993), and araneophagy, or preying on other spiders. Although the monophyly of the subfamily is now accepted (Agnarsson 2004), relationships between genera are poorly understood.

Until recently, taxonomic studies on native spiders in the Hawaiian Islands were derived almost entirely from the collections of R.C.L. Perkins (1913), based upon which Simon (1900) described 77 species endemic to the islands. Simon also recognized the speciose nature of one or a few genera in 4 spider families: Theridiidae, Salticidae, Thomisidae, and Tetragnathidae. More recently, taxonomic studies have been conducted on thomisids (Suman 1970), and the genera *Tetragnatha* Latreille 1804 (Tetragnathidae, Gillespie 1991, 1992, 1994, 2002, 2003) and *Orsonwelles* Hormiga 2002 (Linyphiidae, Hormiga 2002), and a number of recent studies have provided insights into patterns and processes underlying diversification in the genera *Tetra-*

gnatha (Gillespie 2004; Blackledge & Gillespie 2004), *Orsonwelles* (Hormiga et al. 2003), and *Havaika* Prószyński 2002 (Salticidae, Arnedo & Gillespie 2006) in the Hawaiian Islands.

Ariamnes (Theridiidae) have been collected consistently in the Hawaiian Islands over the years, and Rivera (unpublished data) has studied Hawaiian members of the kleptoparasitic genus *Argyrodes* (initially known only by the single species *Argyrodes hawaiiensis* Simon 1900). Within the free-living *Ariamnes*, Simon (1900) recognized a single species, which he described as *A. corniger* Simon 1900. Since that time, there have been no further studies on this group.

Hawaiian representatives of the subfamily Argyrodinae were initially described in the two genera mentioned above, *Argyrodes hawaiiensis* and *Ariamnes corniger*. *Argyrodes hawaiiensis* is a short-bodied kleptoparasite; recent studies indicate that it belongs to a small clade of three species in Hawaii (Rivera unpublished data). *Ariamnes corniger* falls within a clade of multiple species that forms the focus of the current paper. All species show similarity in genitalic structure, yet considerable ecological, and associated morphological, differentiation. The Hawaiian lineage shows considerable morphological difference from other representatives of the genus *Ariamnes* as described in Agnarsson (2004). Rather, the eye arrangement might place it within the genus *Neospintharus*. However, the abdominal shape and genitalic structure (in particular that of the male palp) place it closer to *Rhomphaea*: The arrangement of the primary sclerites (embolus, conductor, median apophysis, theridiid tegular apophysis) of the male palp of *Rhomphaea* (Agnarsson 2004) is similar to that of the Hawaiian *Ariamnes* (Fig. 96). Simon (1900) commented on *A. corniger* as follows (in translation): "This remarkable species falls between the genera *Ariamnes* and *Rhomphaea*; it is related to the first by its narrow and vertical clypeus and the cylindrical femur and tibia of the palps; but the tibia of the forelegs is at least as long as the metatarsus, resembling more those of *Rhomphaea*. Its ocular area is provided, even in the female (only known sex), with a conical median tubercle, a character common to several *Rhomphaea* but up to now unknown in *Ariamnes*." Upon discovery of a male, Simon (1904) add-

ed "*A. corniger*, E Simon, is intermediate between the genera *Ariamnes* and *Rhomphaea* and could with almost as much justification be assigned to the one as to the other. The sexual characters also resemble those of unquestionable *Argyrodes*." Preliminary molecular data (M.A.J. Rivera and R.G. Gillespie, unpublished data) from specimens in the genera *Argyrodes*, *Rhomphaea*, *Ariamnes*, and *Neospintharus* indicate no tight affinity with any of these groups. In summary, the affinities of the long-bodied Hawaiian Argyrodinae are currently unknown; accordingly, we continue with the currently accepted generic assignment to the genus *Ariamnes*.

Ariamnes in the Hawaiian Islands are exclusively nocturnal and most frequently found free-living. However, it is not uncommon also to find them in kleptoparasitic association with a host spider, with members of the endemic Hawaiian genus *Orsonwelles* being the only known hosts to date. The following species have been found as kleptoparasites on the webs of different species of *Orsonwelles*: *A. kahili*, *A. makue*, *A. melekakimaka* and *A. laau*. These species are also found as free-living individuals. It appears, therefore, that kleptoparasitism is facultative, unlike representatives of the *Argyrodes* and *Cancellatus* species groups in which it appears to be obligate, but perhaps more like members of the *Trigonum* (= *Neospintharus*) species group in which at least *A. trigonum* shows remarkable versatility (Cangialosi 1997). In terms of prey-catching behavior, the Hawaiian *Ariamnes* have been observed to catch their spider prey with a net held in their back legs (M. Whitehouse, pers. comm.) similar to the manner reported for *Rhomphaea* (Whitehouse 1987) and *Ariamnes attenuatus* (Eberhard 1979).

The Hawaiian *Ariamnes* are generally elongate, though there is some variability in the relative elongation of the abdomen which can be almost triangular in side view (*A. alepeleke*, *A. huinakolu* and *A. melekakimaka*) with no great extension behind the spinnerets, to thin with considerable elongation behind the spinnerets (all other species described). The legs are also quite variable in length, though all show the leg formula of 1423 characteristic of most argyrodines (Agnarsson 2004). For example, in *A. corniger*, the female leg I measures 24 mm ($3.8 \times$ length of abdomen), leg II 14 mm, leg III 8 mm, and leg IV 20 mm.

METHODS

Characters examined.—Morphological measurements taken were the same as those described in Exline & Levi (1962): the shape of the head and clypeus of the male, and the shape of the abdomen and genitalia. Species are described in order of geographic locality from Kauai (the oldest island) through Oahu, Molokai, Maui, and Hawaii (youngest island).

Terminology.—Unless indicated otherwise, all measurements are in mm. All holotypes and allotypes have been deposited in the Bishop Museum, Honolulu, Hawaii (BPBM) and all paratypes will be deposited in the Es-

sig Museum of Entomology of the University of California, Berkeley, California (EMUC).

TAXONOMY

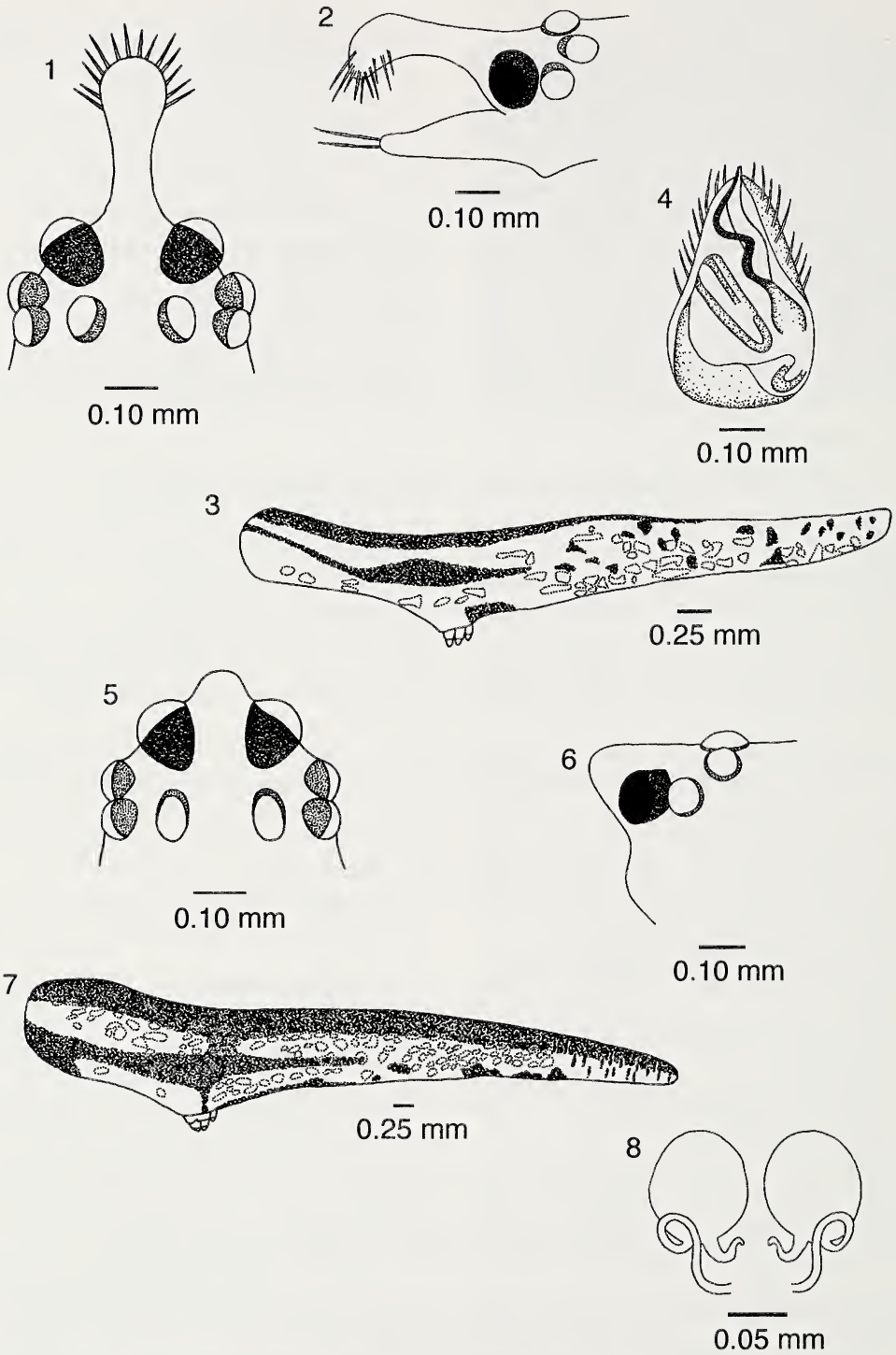
Family Theridiidae Sundevall 1833
Subfamily Argyrodoinae
Exline and Levi 1962
Genus *Ariamnes* Thorell 1869

Ariadne Doleschall 1857:410 (preoccupied by *Ariadna* Audouin 1826).
Ariamnes Thorell 1869:37 (replacement name for *Ariadne* Doleschall 1859).

Type species.—*Ariadne flagellum* Doleschall 1857, by monotypy.

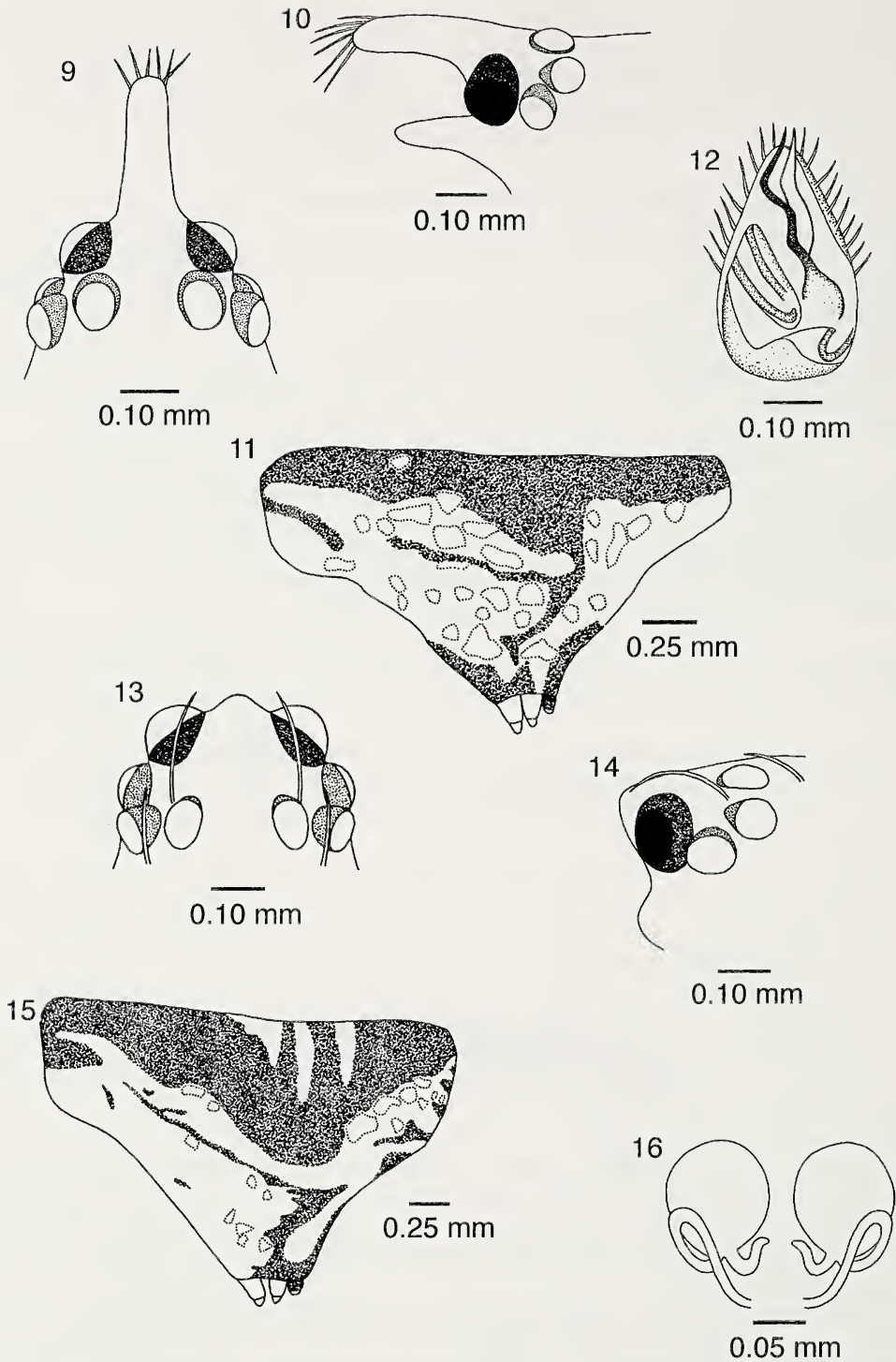
KEY TO HAWAIIAN LONG-BODIED *ARIAMNES* SPECIES

- 1. Males 2
Females 12
- 2. Embolus with large, looping, distal undulation (Figs. 89–91, 94, 100) 3
Embolus straight or with very shallow undulations (Figs. 92, 93, 95–99) 7
- 3. Abdomen short, extension behind spinnerets shorter than section in front; high, height approximately 50% length; shape triangular (Fig. 11) *Argyroides huinakolu* new species
Abdomen longer, extension behind spinnerets much greater than section in front (Fig. 3) 4
- 4. Abdomen much higher at spinnerets, height about a third of length (Fig. 43); rectangular area separating cephalic and clypeal processes (Fig. 42); conductor less projecting, much shorter than embolus (Fig. 44) *Argyroides melekakimaka* new species
Maximum abdominal height \leq 20% length; “U” or “V” shaped area separating cephalic and clypeal processes; conductor as long or longer than embolus 5
- 5. Conductor long, thread-like, distally projecting, much longer than embolus and not closely aligned with it at tip (Figs. 84, 100) *Argyroides hiwa* new species
Conductor and embolus similar in length 6
- 6. Cephalic process short (13% carapace length), thick, straight, not distended at tip (Fig. 18) *Argyroides makue* new species
Cephalic process longer (16% carapace length), thinner stalk, curved over and distended at tip (Fig. 2) *Argyroides kahili* new species
- 7. Embolus with shallow undulations (Figs. 92, 95–97); abdomen covered with densely packed silver blocks 8
Embolus without noticeable undulations, at most shallow, screw-like twists (Figs. 93, 98, 99) 10
- 8. Abdomen length $> 2.5 \times$ carapace length (Fig. 27); proximal and distal undulations of embolus of similar height with tip angled parallel to conductor (Figs. 28, 92) *Argyroides uwepa* new species
Abdomen length $< 2.3 \times$ carapace length; proximal undulation of embolus of greater height than distal, and/or tip angled away from conductor 9
- 9. Opening between cephalic and clypeal process greatest at distal end with cephalic and clypeal setae angled towards each other (Fig. 58); total length approximately 5.0 mm ... *Argyroides alepeleke* new species
Opening between cephalic and clypeal process similar at distal and proximal end with cephalic and clypeal setae approximately at right angles to each other (Fig. 50); total length approximately 6.5 mm *Argyroides corniger* Simon

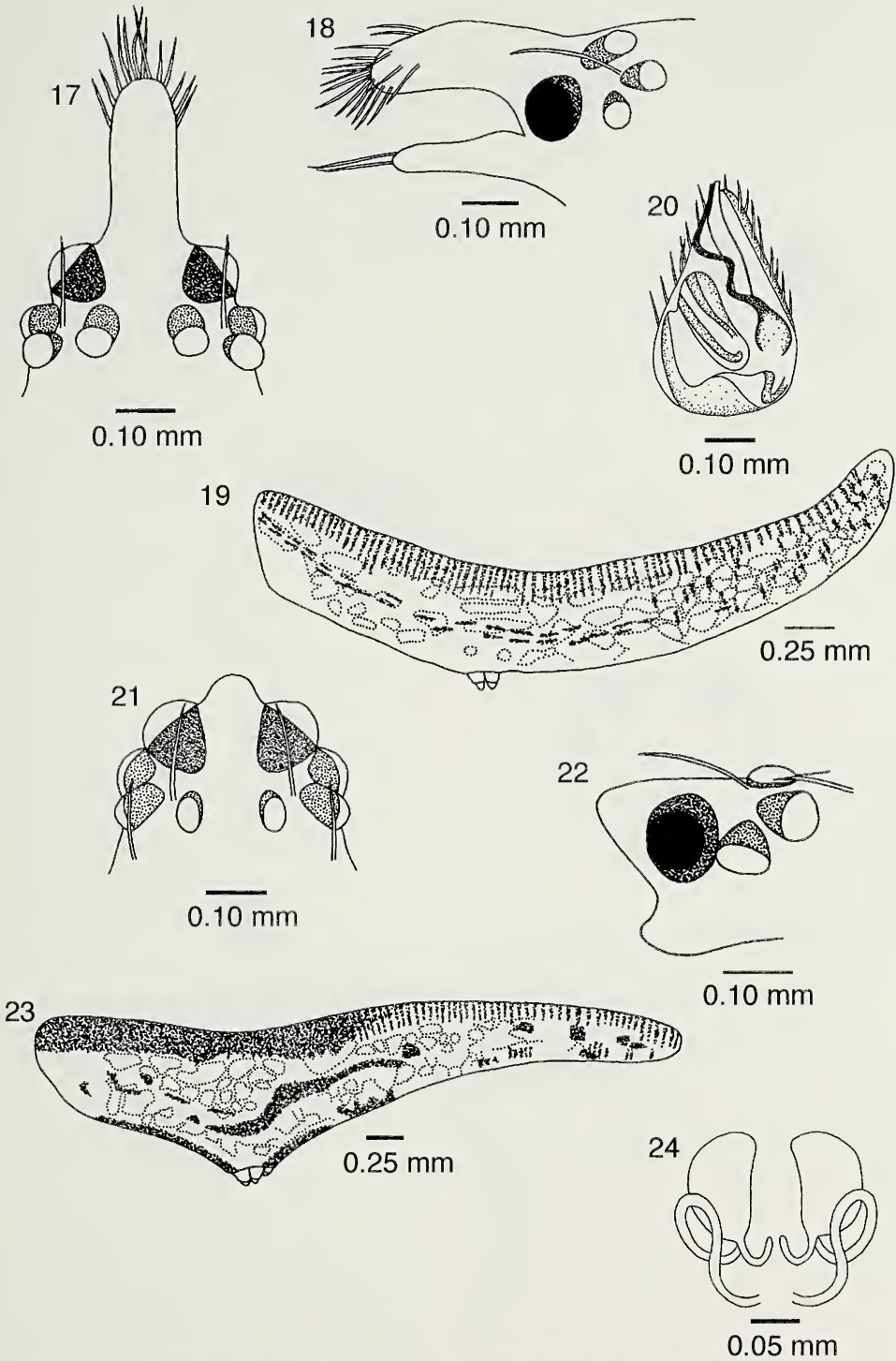


Figures 1-8.—*Ariamnes kahili* new species: 1-4, male holotype; 5-8, female allotype. 1. Cephalic process, dorsal view; 2. Cephalic and clypeal processes, lateral view; 3. Abdomen, lateral view; 4. Left palpus, ventral view; 5. Cephalic area, dorsal view; 6. Cephalic and clypeal area, lateral view; 7. Abdomen, lateral view; 8. Vulva, dorsal view.

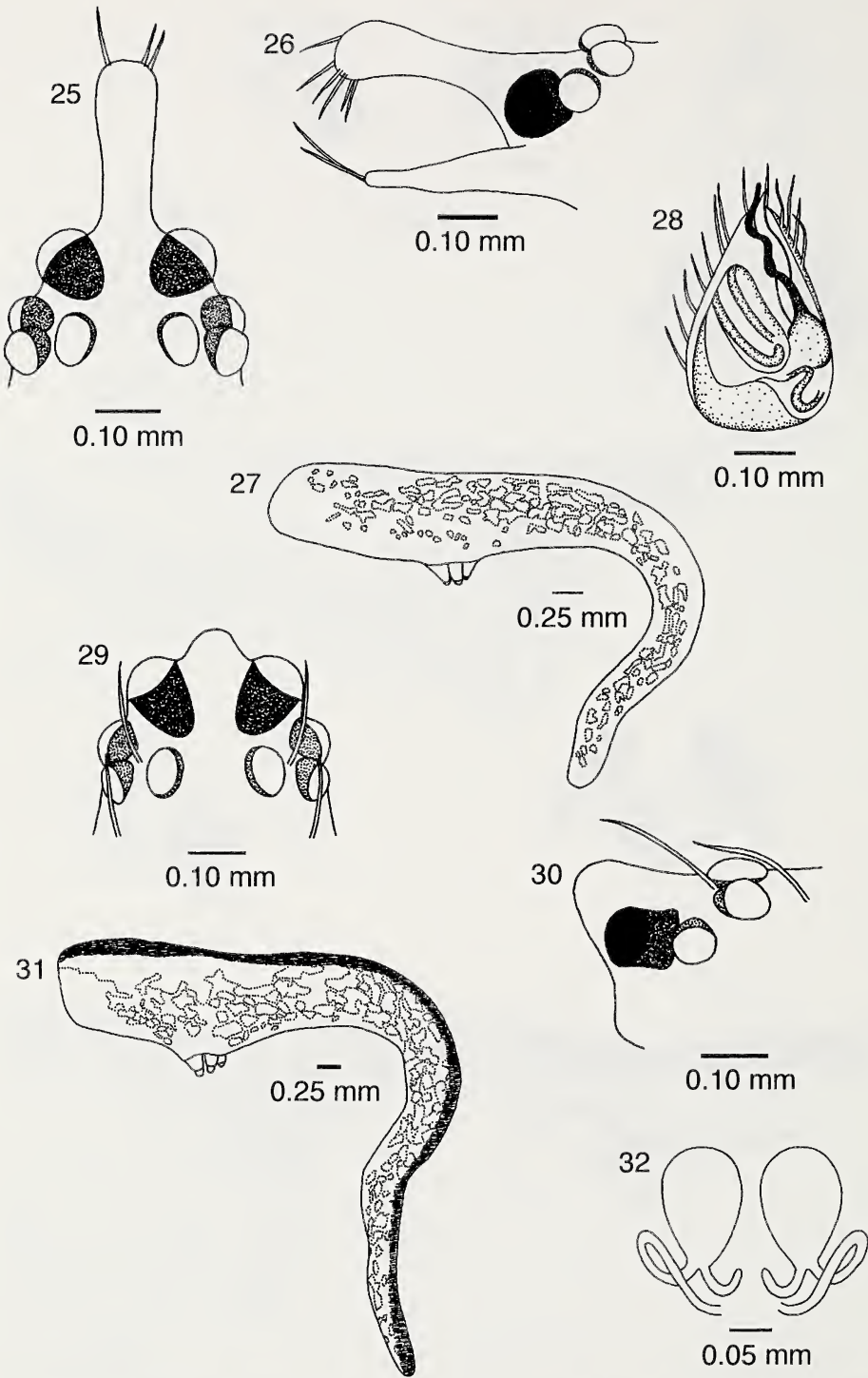
10. Cephalic process very long (approximately 20% length of carapace), curved over and not noticeably distended at tip (Fig. 74); abdomen densely covered in silver blocks; carapace pale with dark lines on either side of midline	<i>Argyrodes waikula</i> new species	
Cephalic process short (approximately 15% length of carapace), straight or very slightly curved over; abdomen dark with variable scattered silver blocks; carapace dark with lighter midline		11
11. Embolus almost straight (Figs. 68, 98); abdomen with silver blotches on black blotches on dorsal surface as well as on sides	<i>Argyrodes laau</i> new species	
Twists in embolus quite pronounced (Figs. 36, 93); abdomen very dark black on dorsal surface	<i>Argyrodes poele</i> new species	
12. Abdominal height > 45% length (Fig. 15, 47, 63)		13
Abdominal height approximately < 45% length (Fig. 55)		15
13. Abdominal height approximately 60–65% length, short, approximately 2.5–3.5 mm (Fig. 15); cephalic and clypeal processes similar in size (Fig. 14); coloration of abdomen in dorsal area very dark, tan below with numerous silver and black flecks	<i>Argyrodes huinakolu</i> new species	
Abdominal height approximately 45–55% length, short, approximately 3.5–6.0 mm; cephalic process > 3 × size of clypeal process (Figs. 46, 62). Abdomen fairly uniformly colored with silver blocks		14
14. Cephalic process projecting well in front of AMEs by almost width of AMEs (Fig. 46); abdomen brown fairly loosely covered with silver blocks	<i>Argyrodes melekalikimaka</i> new species	
Cephalic process barely projecting at all (by < 50% width of AMEs) in front of AMEs (Fig. 62); abdomen densely covered with silver blocks, sometimes with red superimposed	<i>Argyrodes alepeleke</i> new species	
15. Abdomen much higher at spinnerets than half way between spinnerets and posterior end (2.3–3.5 × as high) (Figs. 55, 79); abdomen covered all over with large silver blocks		16
Abdomen only slightly higher at spinnerets than half way between spinnerets and posterior end (1.4–2.0 as high) (Fig. 7)		17
16. Cephalic process projecting well in front of AMEs by almost width of AMEs (Fig. 54); duct of vulva loosely coiled (Fig. 56)	<i>Argyrodes corniger</i> Simon	
Cephalic process less projecting (by < 50% width of AMEs) in front of AMEs (Fig. 78); duct of vulva in a tight loop (Fig. 80)	<i>Argyrodes waikula</i> new species	
17. Abdomen very long and thin, height only approx 15% length (Figs. 7, 31, 87)		18
Abdomen height > 20% length (Figs. 23, 39, 71)		20
18. Spinnerets close to anterior, > 75% of abdomen behind spinnerets (Fig. 31); abdomen covered all over with blocks of silver	<i>Argyrodes uwepa</i> new species	
Spinnerets not as close to anterior, < 70% of abdomen behind spinnerets (Figs. 7, 87); abdomen with some black flecks		19
19. Posterior eye row straight (Fig. 5); abdomen covered all over with small silver blocks and black flecks; epigynal aperture almost round (Fig. 101)	<i>Argyrodes kahili</i> new species	
Posterior margin of posterior eye row procurved (Fig. 85); abdomen with dark dorsal area, remainder covered all over with small silver blocks and black flecks; epigynal aperture transverse ellipse (Fig. 111)	<i>Argyrodes hiwa</i> new species	
20. Spinnerets close to anterior, approximately 75% of abdomen behind spinnerets (Fig. 71); abdomen dark streaked with silver blotches	<i>Argyrodes laau</i> new species	
Spinnerets further down abdomen, < 65% of abdomen behind spinnerets		21
21. Cephalic process pronounced and pointed (Fig. 22); abdomen dark on dorsal surface, packed with silver blocks with black flecks below	<i>Argyrodes makue</i> new species	
Cephalic process short and rounded (Fig. 38); abdomen silver and black but very dark	<i>Argyrodes poele</i> new species	



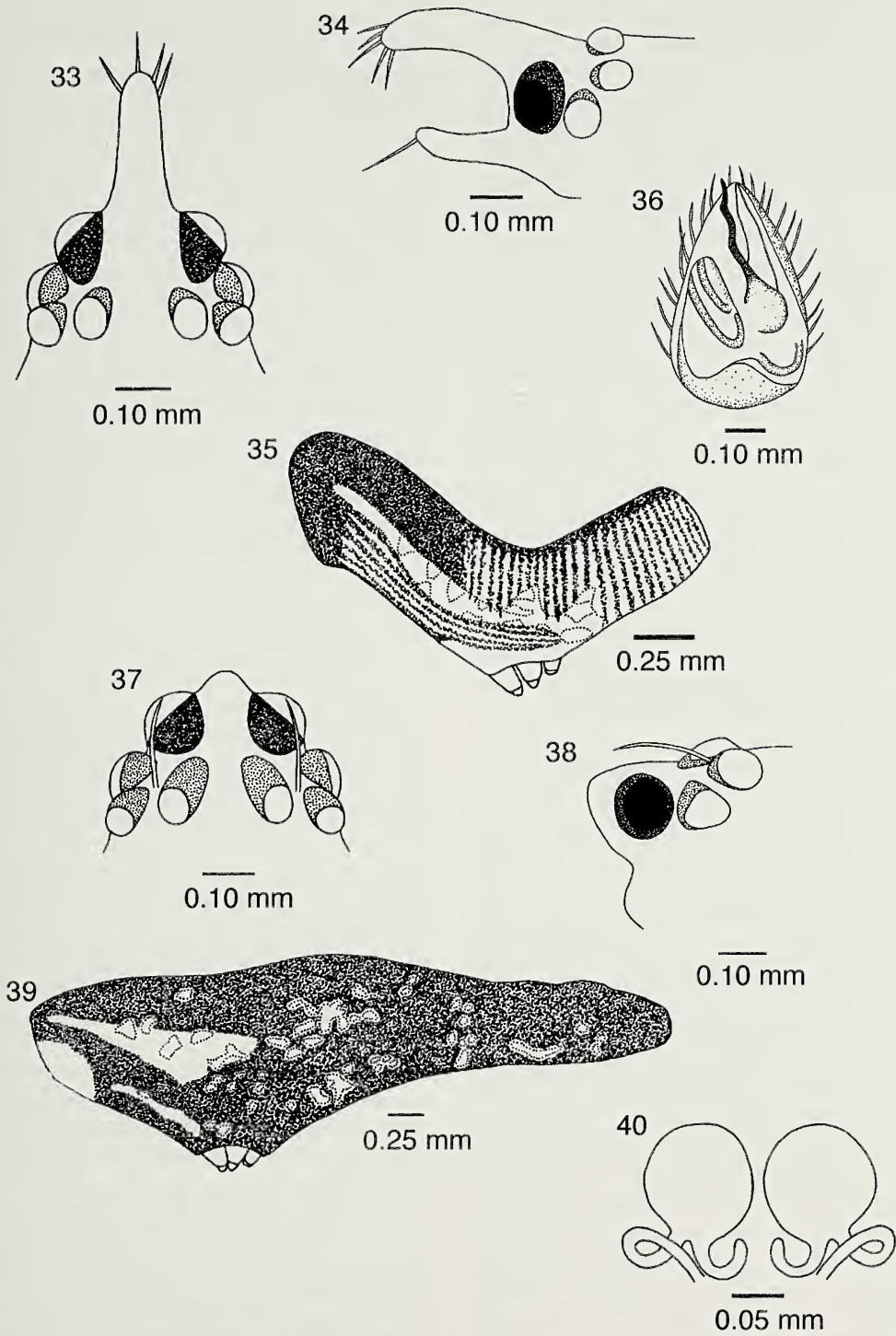
Figures 9–16.—*Ariamnes huinakolu* new species: 9–12, male holotype; 13–16, female allotype. 9. Cephalic process, dorsal view; 10. Cephalic and clypeal processes, lateral view; 11. Abdomen, lateral view; 12. Left palpus, ventral view; 13. Cephalic area, dorsal view; 14. Cephalic and clypeal area, lateral view; 15. Abdomen, lateral view; 16. Vulva, dorsal view.



Figures 17–24.—*Ariamnes makue* new species: 17–20, male holotype; 21–24 female allotype. 17. Cephalic process, dorsal view; 18. Cephalic and clypeal processes, lateral view; 19. Abdomen, lateral view; 20. Left palpus, ventral view; 21. Cephalic area, dorsal view; 22. Cephalic and clypeal area, lateral view; 23. Abdomen, lateral view; 24. Vulva, dorsal view.



Figures 25–32.—*Ariamnes uwepa* new species: 25–28, male holotype; 29–32, female allotype. 25. Cephalic process, dorsal view; 26. Cephalic and clypeal processes, lateral view; 27. Abdomen, lateral view; 28. Left palpus, ventral view; 29. Cephalic area, dorsal view; 30. Cephalic and clypeal area, lateral view; 31. Abdomen, lateral view; 32. Vulva, dorsal view.



Figures 33–40.—*Ariamnes poele* new species: 33–36, male holotype; 37–40, female allotype. 33. Cephalic process, dorsal view; 34. Cephalic and clypeal processes, lateral view; 35. Abdomen, lateral view; 36. Left palpus, ventral view; 37. Cephalic area, dorsal view; 38. Cephalic and clypeal area, lateral view; 39. Abdomen, lateral view; 40. Vulva, dorsal view.

Ariamnes kahili new species

Figs. 1–8, 89, 101, 112

Type specimens.—USA: *Hawaiian Islands*: holotype male, allotype female, Kauai, Mt. Kahili, 670 m elev., 21.99°N, 159.49°W, 20 December 1997, A. Asquith (BPBM); 1 paratype male, Kauai, Mohihi Ditch, 1067 m elev., 22.12°N, 159.63°W, 19 February 1991, R. Gillespie (EMUC); 1 paratype female, Kokee, 1097 m elev., 22.13°N, 159.65°W, in vegetation, 26 June 1964, D.E. Hardy, (BPBM).

Etymology.—The specific epithet, regarded as a noun in apposition, is from the type locality of the species on Kauai.

Diagnosis.—*Ariamnes kahili* can be distinguished from most other species based on the deep undulations of the embolus of the male palp, projecting above the cymbium in parallel with the conductor (Fig. 4, 89). Similar palps are found in *A. huinakolu* and *A. makue*. Compared to *A. makue*, the cephalic process in *A. huinakolu* is longer and distended at tip; the abdomen is much longer ($2.3 \times$ length of carapace, compared to approximately $1.4 \times$ in *A. huinakolu* and $1.7 \times$ in *A. makue*).

Description.—*Holotype male* (Figs. 1–4, 89): Carapace dark brown with light band running longitudinally down middle. Abdomen dull light brown with numerous very loosely packed small silver blocks and black streaks running longitudinally in a line along side from front, turning into scattered black specks behind spinnerets (Fig. 3). Posterior eyes separated by $1.5 \times$ diameter (Fig. 1). Cephalic process 16% length of carapace, tip distended with numerous setae (Fig. 2). Clypeal process 80% length of cephalic process, narrowing at tip where there are several long setae. Abdomen uniformly elongate, only $\sim 1.5 \times$ higher at spinnerets than half way between the spinnerets and posterior end (Fig. 3). Abdomen 5.0 mm length, 70% of this posterior to spinnerets. Carapace 2.1 mm length, 1.1 mm width. Palp (Figs. 4, 89): Embolus with deep undulations, projecting well above cymbium, closely aligned with conductor along length; conductor (membranous) same length as embolus.

Allotype female (Figs. 5–8, 101, 112): Color similar to male. Posterior eyes separated by $1.9 \times$ diameter (Fig. 5). Cephalic process 5% length of carapace, clypeal process indistinct,

rounded area (Fig. 6). Abdomen uniformly elongate, only $\sim 1.5 \times$ higher at spinnerets than half way between the spinnerets and posterior end (Fig. 7). Abdomen 8.6 mm length, 70% of this posterior to spinnerets. Carapace 2.1 mm length, 1.1 mm width. Vulva (Fig. 8): Receptacles spherical, ducts looped in figure-eight. In external view, epigynal area almost round with larger dark ring around central area (Fig. 101) with hooked scape (Fig. 112).

Variation.—Total length varies 6.5–7.1 mm in males, 10.7–11.3 mm in females, due to variable elongation in the abdomen. Color in life is quite variable; most individuals collected had a bright iridescent gold abdomen, but some had extensive dark markings.

Natural history.—*Ariamnes kahili* is found in wet forest habitats on the island of Kauai. The species appears to be largely free-living, but has been found on the webs of *Orson-welles*.

Ariamnes huinakolu new species

Figs. 9–16, 90, 102, 113

Type specimens.—USA: *Hawaiian Islands*: holotype male, Kauai, Makaleha Mountains, 950 m elev., 22.13°N, 159.42°W, 28 April 2000, M. Arnedo, G. Hormiga (BPBM); allotype female, Kauai, Makaleha Mountains, 950 m elev., 22.13°N, 159.42°W, 19 April 1999, M. Arnedo, G. Hormiga, N. Scharff (BPBM); 1 paratype male, Kauai, Kahili Mountain, 920 m elev., 21.98°N, 159.50°W, March 1998 (EMUC); 1 paratype female, Haupu, 700 m elev., 21.93°N, 159.40°W, 30 April 2000, M. Arnedo, G. Hormiga, A. Asquith (EMUC).

Etymology.—The specific epithet, regarded as a noun in apposition, is from the Hawaiian word “huinakolu” meaning triangle, and refers to the almost equilateral triangular shape to the abdomen.

Diagnosis.—*Ariamnes huinakolu* can be readily distinguished from all other species based on the very high and short abdomen (height approximately 52% length in males, 63% in females) (Figs. 11, 15).

Description.—*Holotype male* (Figs. 9–2, 90): Carapace dark brown with creamy elongate oval area running longitudinally down middle. Abdomen dark dorsally, tan below midline with silver flecks at border between dark and tan areas (Fig. 11). Lower tan area

with black lines and flecks together with sparse silver blocks. Posterior eyes separated by $1.6 \times$ diameter (Fig. 9). Cephalic process 15% length of carapace, not noticeably distended, with numerous setae at tip (Fig. 10). Clypeal process 64% length of cephalic process. Abdomen short, triangular from side, uniformly elongate, only $\sim 1.5 \times$ higher at spinnerets than half way between the spinnerets and posterior end (Fig. 11). Abdomen 2.2 mm length, 40% of this posterior to spinnerets. Carapace 1.5 mm length, 0.9 mm width. Palp (Fig. 12, 90): Embolus with deep undulations, projecting well above cymbium, parallel to conductor along length; conductor (membranous) thin, same length as embolus.

Allotype female (Figs. 13–16, 102, 113): Color similar to male. Posterior eyes separated by $2.9 \times$ diameter (Fig. 13). Cephalic process 3% length of carapace, clypeal process similar in size and shape (Fig. 14). Abdomen short and high, $\sim 1.5 \times$ higher at spinnerets than half way between the spinnerets and posterior end (Fig. 15). Abdomen 2.7 mm length, 30% of this posterior to spinnerets. Carapace 1.7 mm length, 1.1 mm width. Vulva (Fig. 16): Receptacles spherical, ducts looped in figure-eight. In external view, epigynal area almost round with dark patch surrounding anterior area (Fig. 101) and with small pointed scape (Fig. 112).

Variation.—Total length varies 3.4–3.7 mm in males, 3.5–4.4 mm in females. Specimens have been found from a single locality only, and little is known as to how much variation exists.

Natural history.—*Ariamnes huinakolu* has been found mainly on the summit of the Makaleha Mountains on Kauai. It is largely restricted to this area, a site of wet forest on the summit of an isolated mountain. Kleptoparasitic tendencies are unknown.

Ariamnes makue new species

Figs. 17–24, 91, 103, 114

Type specimens.—USA: *Hawaiian Islands*: holotype male, Oahu, Waianae Mountains, Puu Kaua, South Gulch, Honouliuli Preserve, 580 m elev., 21.45°N, 158.10°W, 6 August 1998, M. Arnedo, C. Ewing (BPBM); allotype female, Oahu, Waianae Mountains, Palikea, Honouliuli Preserve, 610 m elev., 21.43°N, 158.83°W, 20 August 1995, R. Gillespie, G. Roderick (BPBM); 1 paratype fe-

male, Oahu, Waianae Mountains, Puu Kaua, South Gulch, Honouliuli Preserve, 580 m elev., 21.45°N, 158.10°W, 6 August 1998, M. Arnedo, C. Ewing (EMUC); 1 paratype male, Oahu, Mount Kaala, 550 m elev., 21.52°N, 158.15°W, on large webs of *Orsonwelles* sp. (Linyphiidae), 23 September 1996, M. Rivera & G. Roberts (EMUC).

Etymology.—The specific epithet, regarded as a noun in apposition, is from the Hawaiian word “māku‘e” meaning a dark color, and refers to the very dark color of the abdomen of this species.

Diagnosis.—*Ariamnes makue* can be distinguished from all other species based on the deep undulations of the embolus (Fig. 91) and the relatively short posterior end of the abdomen (Figs. 19, 23).

Description.—*Holotype male* (Figs. 17–20, 91): Carapace dark with lighter longitudinal band running down midline. Abdomen with dark band running along dorsal surface (Fig. 19). Brownish below with loosely packed silver blocks and black longitudinal flecks along sides. Posterior eyes separated by $1.6 \times$ diameter (Fig. 17). Cephalic process 13% length of carapace, thick but not noticeably distended, with numerous setae at tip (Fig. 18). Clypeal process 84% length of cephalic process. Abdomen uniformly elongate, only $\sim 1.1 \times$ higher at spinnerets than half way between the spinnerets and posterior end (Fig. 19). Abdomen 3.6 mm length, 60% of this posterior to spinnerets. Carapace 2.1 mm length, 1.0 mm width. Palp (Figs. 20, 91): Embolus with very deep distal undulation, projecting above cymbium, parallel to conductor along length; conductor same length as embolus.

Allotype female (Figs. 21–24, 103, 114): Color similar to male. Posterior eyes separated by $2.3 \times$ diameter (Fig. 21). Cephalic process 5% length of carapace, similar in shape to (but $3.7 \times$ as long as) clypeal process (Fig. 22). Abdomen elongate, $\sim 1.8 \times$ higher at spinnerets than half way between the spinnerets and posterior end (Fig. 23). Abdomen 4.6 mm length, 63% of this posterior to spinnerets. Carapace 1.7 mm length, 0.9 mm width. Vulva (Fig. 24): Receptacles elongate-oval, ducts looped in figure-eight. In external view, receptacles visible, epigynal area indistinct (Fig. 103) and with scape curved over (Fig. 114).

Remarks.—A male specimen of this species was initially described as a co-type of *A.*

corniger. Simon (1904) stated (in translation): "The frontal tubercle already indicated in the female is much longer, resembling that of *Rhomphaea projiciens* Cambr., from Central America, though it is less dilated and not at all pilous at the end; the second lower tubercle, about half the size, is pointed and directed upward, reminiscent of *Ariamnes bicornis* Cambr., from Brazil." This specimen was examined, and the genitalia found to be very similar to that of *A. makue*. However, the frontal tubercle is considerably longer than any of the Hawaiian *Ariamnes* examined. Without any additional material, it is impossible to determine whether this specimen warrants a separate description.

Variation.—Total length varies 5.3–5.7 mm in males, 5.8–6.3 mm in females, due to variable elongation in the abdomen. Color in life is very dark with little apparent variability.

Natural history.—*Ariamnes makue* is found in mesic forest habitats on the island of Oahu. It has been found on the webs of *Orsonwelles* but can also be free-living; however, microhabitat affinities are unknown.

Ariamnes uwepa new species

Figs. 25–32, 92, 104, 115

Type specimens.—USA: *Hawaiian Islands*: holotype male, Oahu, Koolau Mountains, Poamoho Trail, 600 m elev., 21.52°N, 157.95°W, 18 January 1980, W.C. Gagne (BPBM); allotype female, Oahu, Koolau Mountains, Poamoho Trail, 600 m elev., 21.53°N, 157.95°W, 31 January 1999, R. Gillespie, G. Roderick (BPBM); 1 paratype male, Oahu, Waianae Mountains, Kamaileunu Ridge, north of Puu Kawiwi, 760 m elev., 21.48°N, 158.18°W, 19 October 1975, E.G. Howarth (BPBM); 1 paratype female, Oahu, Waianae Mountains, summer 1966, W. Hay (BPBM).

Etymology.—The specific epithet, regarded as a noun in apposition, comes from the Hawaiian word "uwepa" meaning whip, and refers to the common name often used for the genus *Ariamnes*, with reference to the very elongate and flexible abdomen of these spiders.

Diagnosis.—*Ariamnes uwepa* can be distinguished from other species based on the shallow undulations of the embolus (Figs. 28,

92) and the very long posterior end of the abdomen (Figs. 27, 31).

Description.—*Holotype male* (Figs. 25–28, 92): Carapace quite pale, slightly darker along sides. Abdomen almost solid silver with thin lines of reticulation between blocks (Fig. 27). Posterior eyes separated by $1.5 \times$ diameter (Fig. 25). Cephalic process 16% length of carapace, slightly rounded and blunt at tip, very slightly distended (Fig. 26). Clypeal process 75% length of cephalic process. Abdomen very elongate and narrow, only $\sim 2.0 \times$ higher at spinnerets than half-way between the spinnerets and posterior end (Fig. 27). Abdomen 5.5 mm length, 67% of this posterior to spinnerets. Carapace 1.7 mm length, 0.7 mm width. Palp (Fig. 28, 92): Embolus with two shallow undulations of similar height, projecting slightly above cymbium, parallel to conductor along length; conductor same length as embolus.

Allotype female (Figs. 29–32, 104, 115): Color similar to male. Posterior eyes separated by $1.4 \times$ diameter (Fig. 29). Cephalic process 4% length of carapace, similar in shape to, but $3.7 \times$ as long as, clypeal process (Fig. 30). Abdomen very long and thin, $\sim 2.0 \times$ higher at spinnerets than half way between the spinnerets and posterior end (Fig. 31). Abdomen 8.1 mm length, 76% of this posterior to spinnerets. Carapace 1.9 mm length, 1.0 mm width. Vulva (Fig. 32): receptacles elongate-oval, ducts looped in figure-eight. In external view, receptacles visible, epigynal area indistinct (Fig. 104) and with scape curved over (Fig. 115).

Variation.—Total length varies 6.3–7.2 mm in males, 10.0–10.5 mm in females, due to variable elongation in the abdomen. The abdomen is bright gold in life, sometimes with red marks.

Natural history.—*Ariamnes uwepa* is found in wet and mesic forest habitats on the island of Oahu. Individuals have been collected from beneath leaves in the forest, though little else is known of its natural history.

Ariamnes poele new species

Figs. 33–40, 93, 105, 116

Type specimens.—USA: *Hawaiian Islands*: holotype male, Molokai, Pepeopae boardwalk at night, 1150 m elev., 21.12°N, 156.90°W, 12 May 2000, M. Arnedo, G. Hor-

miga, I. Agnarsson (BPBM); allotype female, Molokai, Kamakou, 1280 m elev., 21.12°N, 156.87°W, 4 June 1997, C.P. Ewing (BPBM); 1 paratype male, 1 paratype female, Maui, Puu Kukui, 1067 m elev., 20.90°N, 156.63°W, 15 January 1998, R. Gillespie, K. Shaw (EMUC); 1 paratype female, Molokai, Upper Kawela Gulch, 1200 m elev., 21.10°N, 156.93°W, 5 January 1981, W.C. Gagne (BPBM).

Etymology.—The specific epithet, regarded as a noun in apposition, is from the Hawaiian word “pō‘ele” meaning black or dark, and refers to the dark color of the abdomen.

Diagnosis.—Male *Ariamnes poele* can be distinguished (especially from *A. corniger* and *A. alepeleke*) based on the embolus which has very shallow undulations and is similar in length to the conductor (Figs. 36, 93). The cephalic projection is relatively short and thinner than in *A. corniger* (Fig. 34 as compared to 50). In both sexes the abdomen is black above with a silver blotched bar along midline of side (Figs. 35, 39).

Description.—*Holotype male* (Figs. 33–36, 93): Carapace dusky black with light line running down midline. Abdomen dark brown/black with silver bar along midline of side (Fig. 35). Legs banded. Posterior eyes separated by $2.0 \times$ diameter (Fig. 33). Cephalic process 19% length of carapace, very slightly curved over at tip, not distended and with numerous robust setae at tip (Fig. 34). Clypeal process 68% length of cephalic process. Abdomen elongate and only $1.4 \times$ higher at spinnerets than half way between the spinnerets and posterior end (Fig. 35). Abdomen 3.4 mm length, 67% of this posterior to spinnerets. Carapace 2.3 mm length, 1.2 mm width. Palp (Figs. 36, 93): embolus fairly long with shallow undulations, projecting slightly above distal margin of cymbium; conductor (membranous) broad, tapering to point, similar in length to embolus.

Allotype female (Figs. 37–40, 105, 116): Color similar to male. Posterior eyes separated by $1.7 \times$ diameter (Fig. 37). Cephalic process 4% length of carapace, slightly more pointed and larger ($3.7 \times$ as long) than clypeal process (Fig. 38). Abdomen fairly long, not high, $\sim 1.7 \times$ higher at spinnerets than half way between the spinnerets and posterior end (Fig. 39). Abdomen 5.9 mm length, 72% of this posterior to spinnerets. Carapace 2.1 mm

length, 1.1 mm width. Vulva (Fig. 40): receptacles large and spherical, ducts looped. In external view, receptacles visible, epigynal area indistinct (Fig. 105) and with scape short and slightly curved (Fig. 116).

Variation.—Total length varies 3.9–4.6 mm in males, 6.6–8.2 mm in females, due to variable elongation in the abdomen. The abdomen is very dark in color with little apparent variability.

Natural history.—*Ariamnes poele* is found in wet forest habitats on the islands of Molokai and Maui (West Maui only). It appears to be largely free-living.

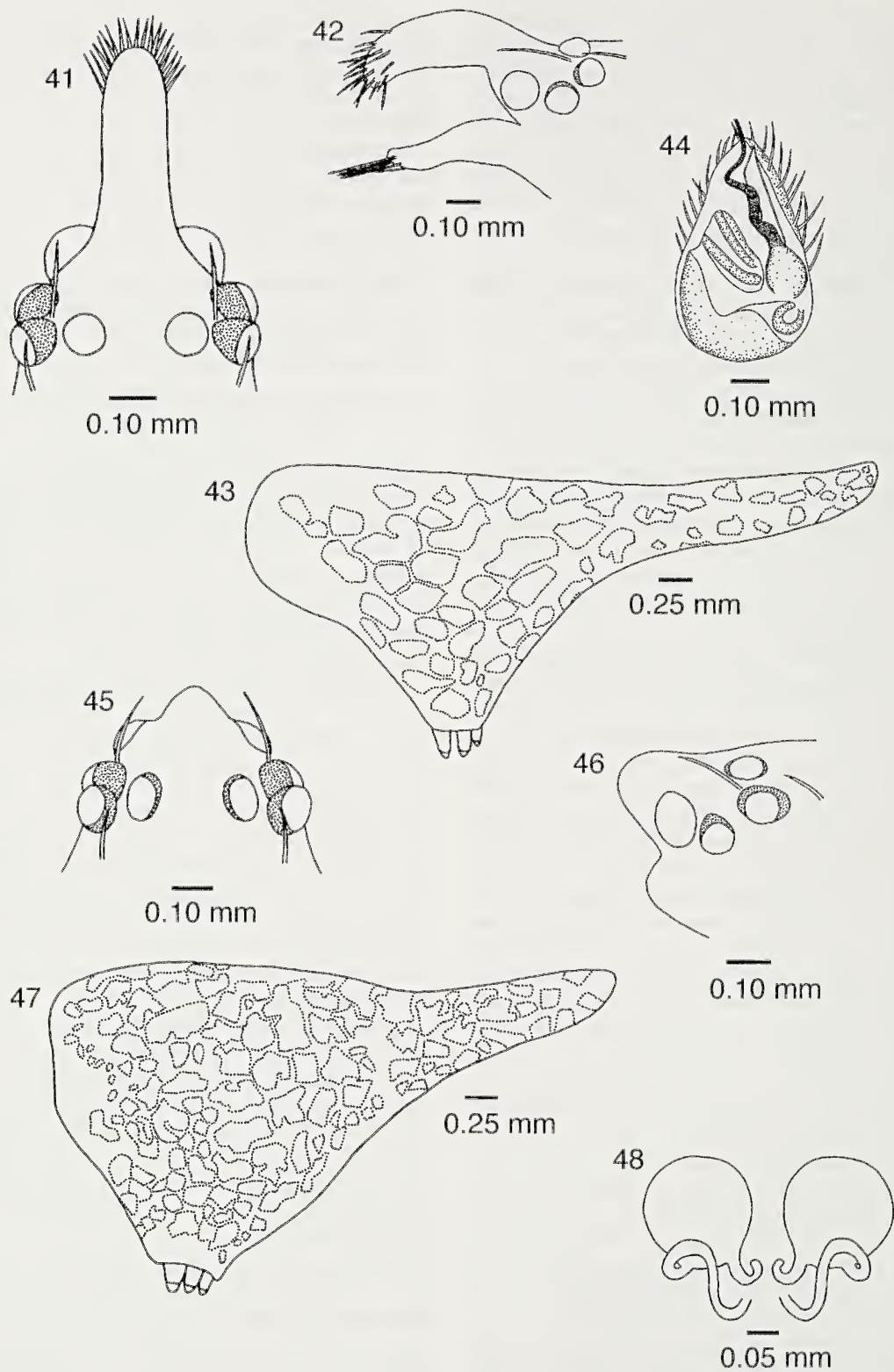
Ariamnes melekalikimaka new species
Figs. 41–48, 94, 106, 117

Type specimens.—USA: *Hawaiian Islands*: holotype male, allotype female, Maui, Puu Kukui, 1067 m elev., 20.90°N, 156.63°W, 15 January 1998, R. Gillespie, K. Shaw (BPBM); 1 paratype female, Molokai, Pepeopae boardwalk at night, 1150 m elev., 21.12°N, 156.90°W, 12 May 2000, M. Arnedo, G. Hormiga, I. Agnarsson (EMUC).

Etymology.—The specific epithet, regarded as a noun in apposition, is from the Hawaiian phrase “Mele Kalikimaka” meaning “Merry Christmas”. The name refers to the color of the animal in life, which is sparkling bright green and red.

Diagnosis.—Male *Ariamnes melekalikimaka* can be distinguished based on the embolus which has a large distal undulation and is much longer and well separated from the conductor (Fig. 44, 94). The form of the cephalic projection is unique, the area separating the cephalic and clypeal processes almost rectangular (usually triangular shaped) (Fig. 42). Females (and to a lesser extent males) are recognized by the relatively short and high abdomen (height 35% length) (Fig. 47). The coloration of the abdomen is also unique, being distinctly marked with a background color of brown (bright green in life), covered all over by loosely packed silver blocks and with red lines and flecks.

Description.—*Holotype male* (Figs. 41–44, 94): Carapace dusky dark with light line running down midline. Abdomen brown (green-brown in life) with rust diamond on the dorsal surface (Fig. 43). Posterior eyes separated by $1.7 \times$ diameter (Fig. 41). Cephalic process 19% length of carapace, angular on inside



Figures 41-48.—*Ariamnes mekalikimaka* new species: 41-44, male holotype; 45-48, female allotype. 41. Cephalic process, dorsal view; 42. Cephalic and clypeal processes, lateral view; 43. Abdomen, lateral view; 44. Left palpus, ventral view; 45. Cephalic area, dorsal view; 46. Cephalic and clypeal area, lateral view; 47. Abdomen, lateral view; 48. Vulva, dorsal view.

border, curved over, thick but not noticeably distended, and with numerous robust setae at tip (Fig. 42). Clypeal process 87% length of cephalic process. Abdomen relatively short and high, $3.4 \times$ higher at spinnerets than half way between the spinnerets and posterior end (Fig. 43). Abdomen 4.9 mm length, 64% of this posterior to spinnerets. Carapace 2.4 mm length, 1.2 mm width. Palp (Figs. 44, 94): embolus very long with deep distal undulation, projecting well above distal margin of cymbium; conductor (membranous) blunt-ended and terminating at edge of cymbium.

Allotype female (Figs. 45–48, 106, 117): Color similar to male. Posterior eyes separated by $2.3 \times$ diameter (Fig. 45). Cephalic process 5% length of carapace, similar in shape but larger ($3.4 \times$ as long) than clypeal process (Fig. 46). Abdomen relatively short and high, $\sim 1.7 \times$ higher at spinnerets than half way between the spinnerets and posterior end (Fig. 47). Abdomen 4.5 mm length, 57% of this posterior to spinnerets. Carapace 2.2 mm length, 1.4 mm width. Vulva (Fig. 48): receptacles large and spherical, ducts in loose figure-eight. In external view, receptacles visible, epigynal area distinct, urn-shaped (Fig. 106), scape almost straight (Fig. 117).

Variation.—Total length varies 6.7–7.3 mm in males, 6.6–7.2 mm in females. The abdomen is brightly colored in life with red marks on iridescent gold.

Natural history.—*Ariamnes melekalikimaka* is found in wet forest habitats at middle elevations on the volcano of Puu Kukui, West Maui, and on Molokai. This species, appears to be largely free-living, but has been found on the webs of *Orsonwelles* sp.

Ariamnes corniger Simon

Figs. 49–56, 95–96, 107, 118

Ariamnes corniger Simon 1900:447, plate XV, fig. 2.

Type specimens.—USA: *Hawaiian Islands*: 1 female syntype, Maui, Haleakala (MNHN); 1 female syntype, Lanai, Koele (MNHN).

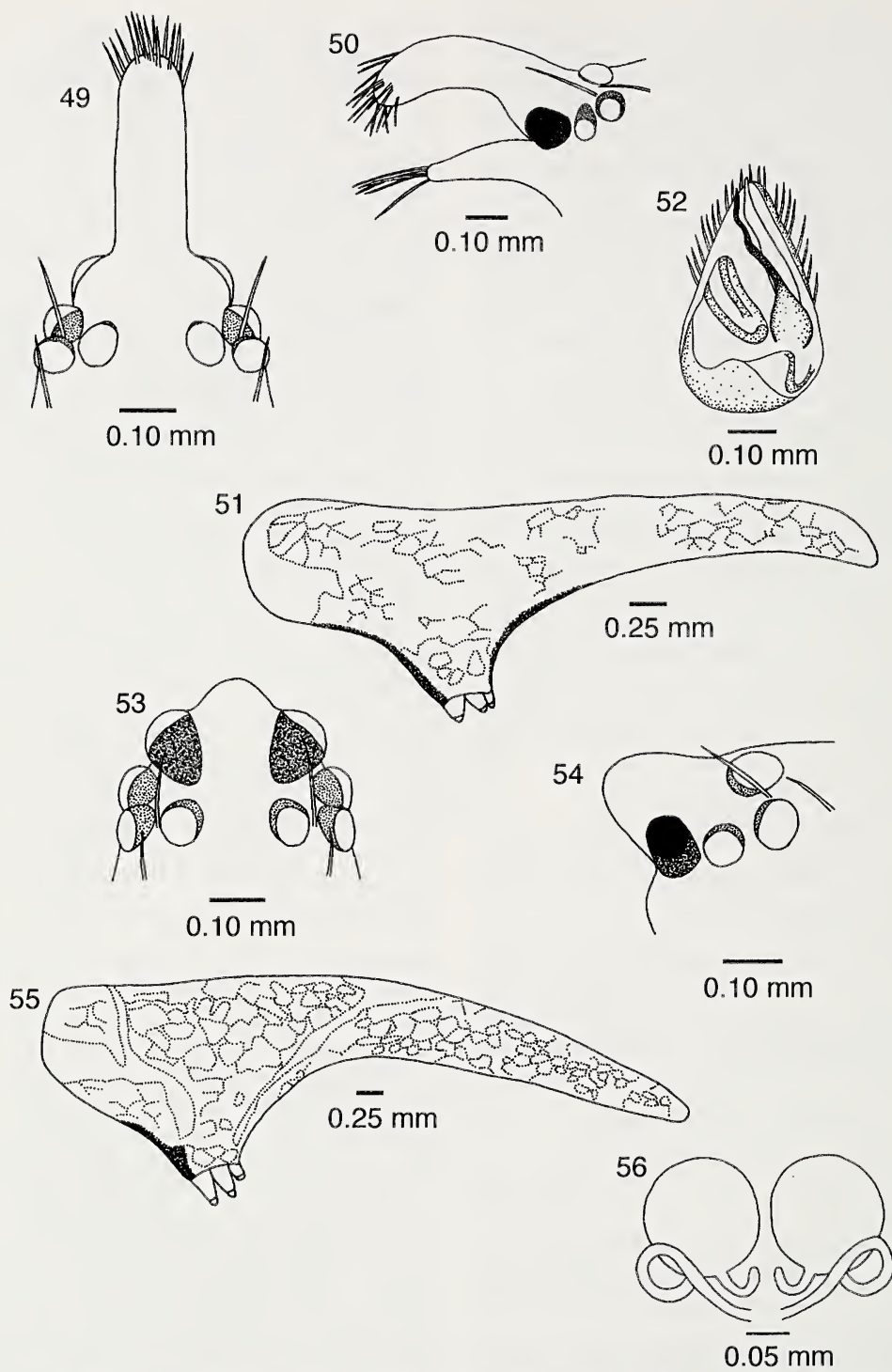
Other material examined.—USA: *Hawaiian Islands*: Maui, Upper Waikamoi Preserve, 1860 m elev., 20.78°N, 156.22°W, 21 November 1997, M. Rivera, B. Thorsby, A. Bohonak, (EMUC); 2 ♂, 2 ♀, Maui, Auwahi, south slope, Haleakala, 1250 m, 20.65°N, 156.35°W, 20 August 1997, R. Gillespie, J. Garb, M.

Heddle (EMUC); 2 ♂, 2 ♀, Maui, Auwahi, south slope, Haleakala, 1524 m elev., 20.65°N, 156.35°W, 4 March 1999, R. Gillespie, A. Medeiros, K. Teramura (EMUC); 2 ♂, 2 ♀, Maui, Kipahulu Valley, 1830 m elev., 20.72°N, 156.13°W, 27 April 1988, A.C. Medeiros (EMUC); 2 ♂, 2 ♀, Maui, bogs on NE. rift of Haleakala, 1676 m elev., 20.73°N, 156.10°W, 15 January 1988, R. Gillespie, A. Medeiros (EMUC).

Diagnosis.—Male *Ariamnes corniger* can be distinguished based on the shallow undulations of the embolus which is the same length as the conductor (Figs. 52, 95–96), and the robust and slightly curved cephalic process (Fig. 50). Both males and females can be recognized based on the anvil-shaped abdomen, much higher at the spinnerets, and the coloration of the abdomen, densely packed with silver blocks (Figs. 51, 55).

Description.—*Male* (Figs. 49–52, 95, 96): Carapace uniformly pale. Abdomen very densely packed all over with silver blocks on a fairly dark background (Fig. 51). Posterior eyes separated by $2.3 \times$ diameter (Fig. 49). Cephalic process robust, 18% length of carapace, slightly curved over, not noticeably distended, and with numerous setae at tip (Fig. 50). Clypeal process 69% length of cephalic process. Abdomen elongate, much higher, $2.8 \times$, at spinnerets than half way between the spinnerets and posterior end (Fig. 51). Abdomen 4.5 mm length, 62% of this posterior to spinnerets. Carapace 2.1 mm length, 1.0 mm width. Palp (Figs. 52, 95, 96): embolus with shallow undulations, projecting above cymbium, roughly parallel to conductor along length; conductor (membranous) broad, tapering to point, same length as embolus.

Female (Figs. 53–56, 107, 118): Color similar to male. Posterior eyes separated by $2.0 \times$ diameter (Fig. 53). Cephalic process 5% length of carapace, similar in shape to, but much more projecting ($4.6 \times$ as long) than clypeal process (Fig. 54). Abdomen anvil-shaped, $\sim 2.8 \times$ higher at spinnerets than half way between the spinnerets and posterior end (Fig. 55). Abdomen 6.2 mm length, 74% of this posterior to spinnerets. Carapace 2.0 mm length, 1.2 mm width. Vulva (Fig. 56): receptacles spherical, ducts tightly looped in figure-eight. In external view, receptacles fairly distinct, epigynal area indistinct (Fig. 107), scape slightly hooked (Fig. 118).



Figures 49–56.—*Ariamnes corniger* Simon: 49–52, male holotype; 53–56, female allotype. 49. Cephalic process, dorsal view; 50. Cephalic and clypeal processes, lateral view; 51. Abdomen, lateral view; 52. Left palpus, ventral view; 53. Cephalic area, dorsal view; 54. Cephalic and clypeal area, lateral view; 55. abdomen, lateral view; 56. Vulva, dorsal view.

Variation.—Total length varies 6.2–6.9 mm in males, 8.0–8.9 mm in females. The abdominal coloration is somewhat variable, ranging from pale gold in the wet forest, to pure white in the dry forest, where it is camouflaged against the white lichen that is found throughout the area.

Natural history.—*Ariamnes corniger* is found on East Maui, where it occurs in both wet forest habitats on the north east slope, and dry forest on the south slope. To date, individuals have been found free living only.

Ariamnes alepeleke new species

Figs. 57–64, 97, 108, 119

Type specimens.—USA: *Hawaiian Islands*: holotype male, allotype female, Maui, Waikamoi Flume, 1250 m elev., 20.90°N, 156.28°W, 8 February 1999, M. Rivera, & A. Rivera (BPBM); 1 paratype female, Maui, Waikamoi Flume, 1250 m elev., 20.82°N, 156.23°W, 13 June 1994, A.M. Tan (EMUC); 1 paratype female, Waikamoi, 1341 m elev., 20.80°N, 156.25°W, 13 August 1994, A.M. Tan (EMUC); 1 paratype male, Makawao Forest Reserve, 1463 m elev., 20.80°N, 156.25°W, under living leaves, 5 October 1979, S.L. Montgomery (BPBM).

Etymology.—The specific epithet, regarded as a noun in apposition, is named after Alepeleke Rivera, the collector of the type species and father of M.A.J. Rivera. Alepeleke is the Hawaiian name for Alfred.

Diagnosis.—Male *Ariamnes alepeleke* can be distinguished based on the shallow undulations of the embolus which barely projects above cymbium (Figs. 60, 97). In both males and females the abdomen is broadly triangular and solid silver (gold in life), sometimes with red superimposed.

Description.—*Holotype male* (Figs. 57–60, 97): Carapace fairly dark at sides, broad, almost white band running down midline. Abdomen very tightly packed all over with silver blocks with little room for reticulation between the blocks (Fig. 59). Ventral area above and anterior to spinnerets flat brownish. Legs uniformly yellow/brown. Posterior eyes separated by $2.5 \times$ diameter (Fig. 57). Cephalic process 20% length of carapace, slightly curved over, not noticeably distended, and with a number of fairly short setae at tip (Fig. 58). Clypeal process 70% length of cephalic process. Abdomen relatively short, slightly

higher, $1.2 \times$, at spinnerets than half way between the spinnerets and posterior end (Fig. 59). Abdomen 3.2 mm length, 50% of this posterior to spinnerets. Carapace 1.8 mm length, 0.9 mm width. Palp (Figs. 60, 97): Embolus with shallow undulations, barely projecting above cymbium, curving away from conductor at tip; conductor broad, blunt-tipped, terminating at edge of cymbium.

Allotype female (Figs. 61–64, 108, 119): Color similar to male. Posterior eyes separated by $2.8 \times$ diameter (Fig. 61). Cephalic process 3% length of carapace, similar in shape to, but larger ($4.3 \times$ as long) than clypeal process (Fig. 62). Abdomen broadly triangular, $\sim 2.0 \times$ higher at spinnerets than half way between the spinnerets and posterior end (Fig. 63). Abdomen 4.7 mm length, 67% of this posterior to spinnerets. Carapace 1.8 mm length, 1.1 mm width. Vulva (Fig. 64): receptacles spherical, ducts with single tight loop. In external view, receptacles and ducts fairly distinct (Fig. 108), scape slightly hooked (Fig. 119).

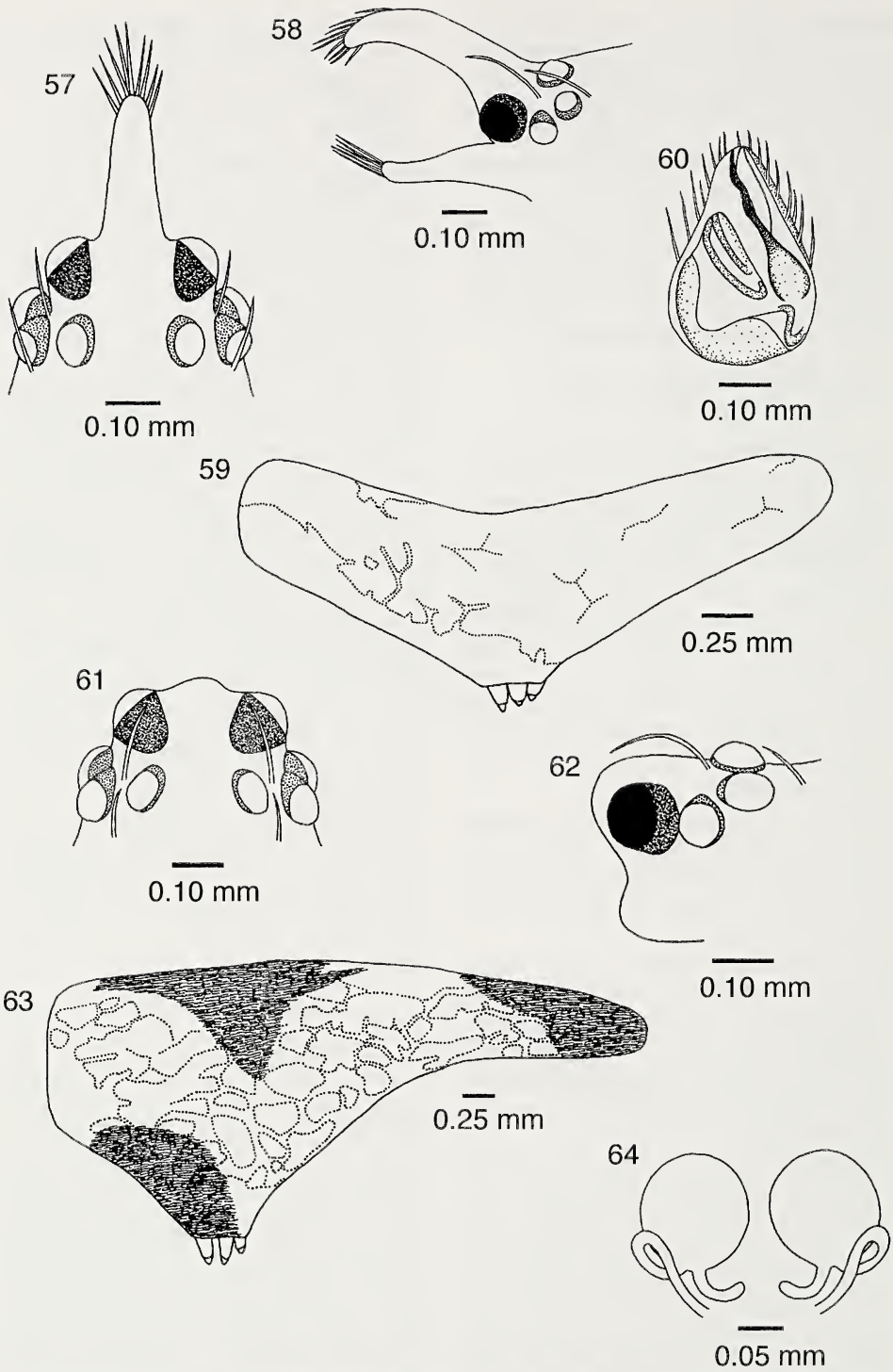
Variation.—Total length varies 4.8–5.0 mm in males, 5.5–6.6 mm in females. This species is bright iridescent gold in life, with variable saddle-shaped red markings on the dorsal surface of the abdomen.

Natural history.—*Ariamnes alepeleke* is found in wet forest habitats at middle elevations on East Maui. To date the species has been found only in free-living state, and usually hangs at night below large leaves in the forest.

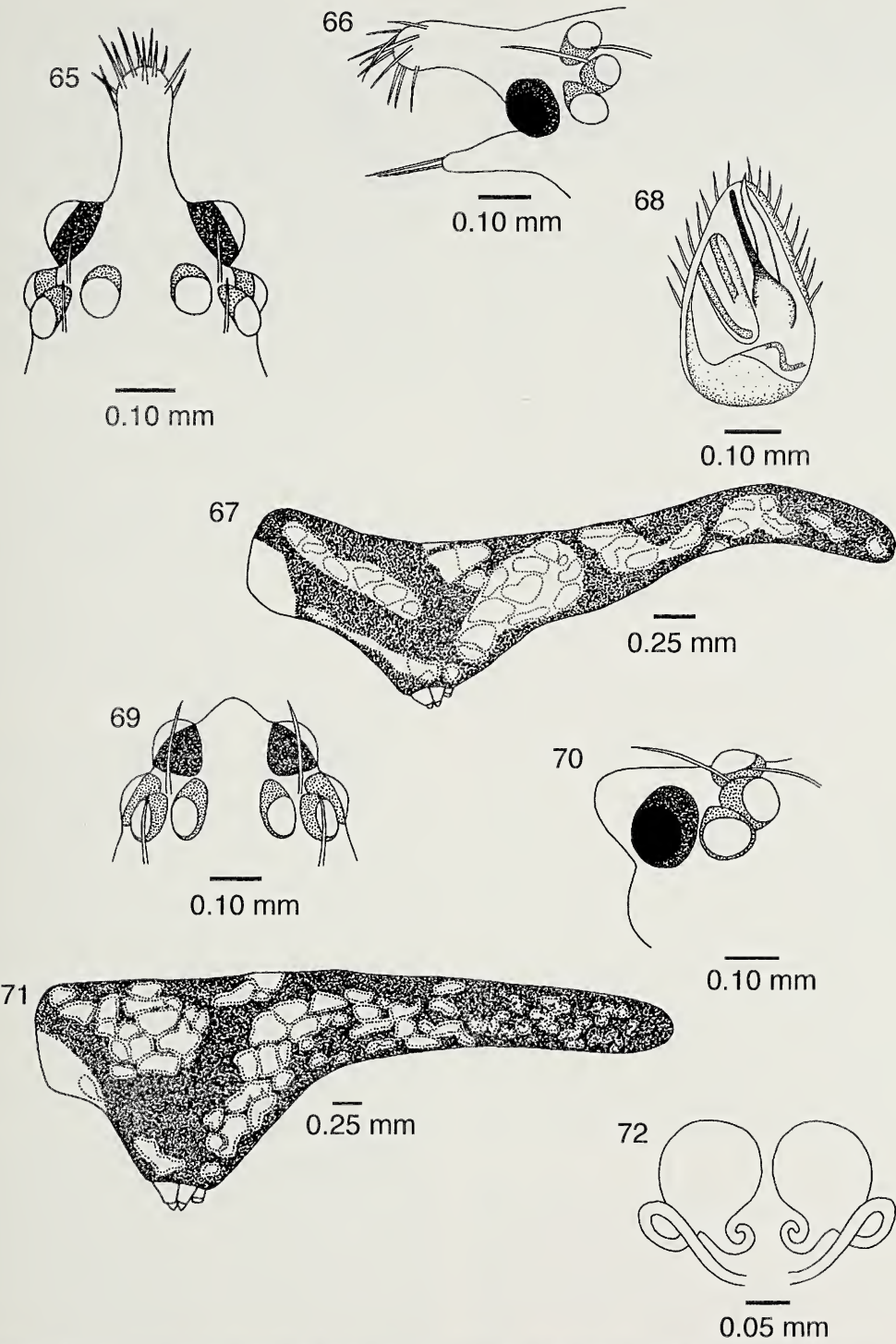
Ariamnes laau new species

Figs. 65–72, 98, 109, 120

Type specimens.—USA: *Hawaiian Islands*: holotype male, Maui, Hanawi Natural Area Reserve, Poouli Cabin, 975 m elev., 20.83°N, 156.13°W, 3 May 1998, J. Liebherr (BPBM); allotype female, Maui, Upper Waikamoi, 1860 m elev., 20.78°N, 156.22°W, 21 November 1997, M. Rivera, B. Thorsby, A. Bohonak (BPBM); 1 paratype male, Maui, Hanawi Natural Area Reserve, Poouli Cabin, 975 m elev., 20.83°N, 156.13°W, 3 May 1998, J. Liebherr (EMUC); 1 paratype female, Maui, Makawao Forest Reserve, 1463 m elev., 20.80°N, 156.25°W, under living leaves, 5 October 1979, S.L. Montgomery (BPBM); 1 paratype male, 1 paratype female, Maui, gulch east of Niania, 2130 m elev., 20.78°N, 156.25°W, swept from *Elaphoglossum hirtum*



Figures 57-64.—*Ariamnes alepeleke* new species: 57-60, male holotype; 61-64, female allotype. 57. Cephalic process, dorsal view; 58. Cephalic and clypeal processes, lateral view; 59. Abdomen, lateral view; 60. Left palpus, ventral view; 61. Cephalic area, dorsal view; 62. Cephalic and clypeal area, lateral view; 63. Abdomen, lateral view; 64. Vulva, dorsal view.



Figures 65–72.—*Ariamnes laau* new species: 65–68, male holotype; 69–72, female allotype. 65. Cephalic process, dorsal view; 66. Cephalic and clypeal processes, lateral view; 67. Abdomen, lateral view; 68. Left palpus, ventral view; 69. Cephalic area, dorsal view; 70. Cephalic and clypeal area, lateral view; 71. Abdomen, lateral view; 72. Vulva, dorsal view.

on shaded stream bank, 6 July 1975, W.C. Gagne (BPBM).

Etymology.—The specific epithet, regarded as a noun in apposition, is from the Hawaiian word “lā‘au” meaning stick, and refers to the common name often used for this group of *Ariamnes*: “stick spiders.”

Diagnosis.—Male *Ariamnes laau* can be distinguished based on the embolus which is almost straight (without undulations) and shorter than the conductor (Figs. 68, 98), the latter barely projecting above the cymbium. Compared to *A. corniger* and *A. alepeleke* the cephalic process is shorter and straight (Fig. 66). In females the extension of the abdomen behind the spinnerets is greater than in *A. alepeleke*, and the difference in height of the abdomen (at spinnerets compared to behind) is much less pronounced than in *A. corniger*. In both sexes the abdomen is black with silver blotches, compared to silver and gold in *A. corniger* and *A. alepeleke* respectively.

Description.—*Holotype male* (Figs. 65–68, 98): Carapace almost black with light line running down midline. Abdomen dark, almost uniformly black on dorsal surface, with silver blotches along sides, decreasing posteriorly (Fig. 67). Legs dark and banded. Posterior eyes separated by $1.4 \times$ diameter (Fig. 65). Cephalic process 14% length of carapace, straight, and slightly distended at tip with numerous robust setae (Fig. 66). Clypeal process 57% length of cephalic process. Abdomen relatively long, $2.4 \times$ higher at spinnerets than half way between the spinnerets and posterior end (Fig. 67). Abdomen 4.2 mm length, 68% of this posterior to spinnerets. Carapace 1.7 mm length, 0.9 mm width. Palp (Figs. 68, 98): embolus almost straight and short, terminating well below distal margin of cymbium; conductor terminating at edge of cymbium, longer than embolus.

Allotype female (Figs. 69–72, 109, 120): Color similar to male. Posterior eyes separated by $2.0 \times$ diameter (Fig. 69). Cephalic process 4% length of carapace, slightly more pointed and larger ($3.4 \times$ as long) than clypeal process (Fig. 70). Abdomen elongate, $\sim 1.5 \times$ higher at spinnerets than half way between the spinnerets and posterior end (Fig. 71). Abdomen 5.4 mm length, 74% of this posterior to spinnerets. Carapace 1.8 mm length, 1.0 mm width. Vulva (Fig. 72): receptacles spherical, ducts with single tight loop. In external view,

receptacles indistinct, epigynal area marked with elongate transverse “ω” (Fig. 109), scape almost straight (Fig. 120).

Variation.—Total length varies 5.2–6.0 mm in males, 7.0–8.3 mm in females, due to variable elongation in the abdomen. The abdomen is very darkly colored with little apparent variability.

Natural history.—*Ariamnes laau* is found in wet forest habitats at middle and high elevations on East Maui. This species appears to be largely free-living, but has been found on the webs of *Orsonwelles* sp; habitat associations are unknown.

Ariamnes waikula new species

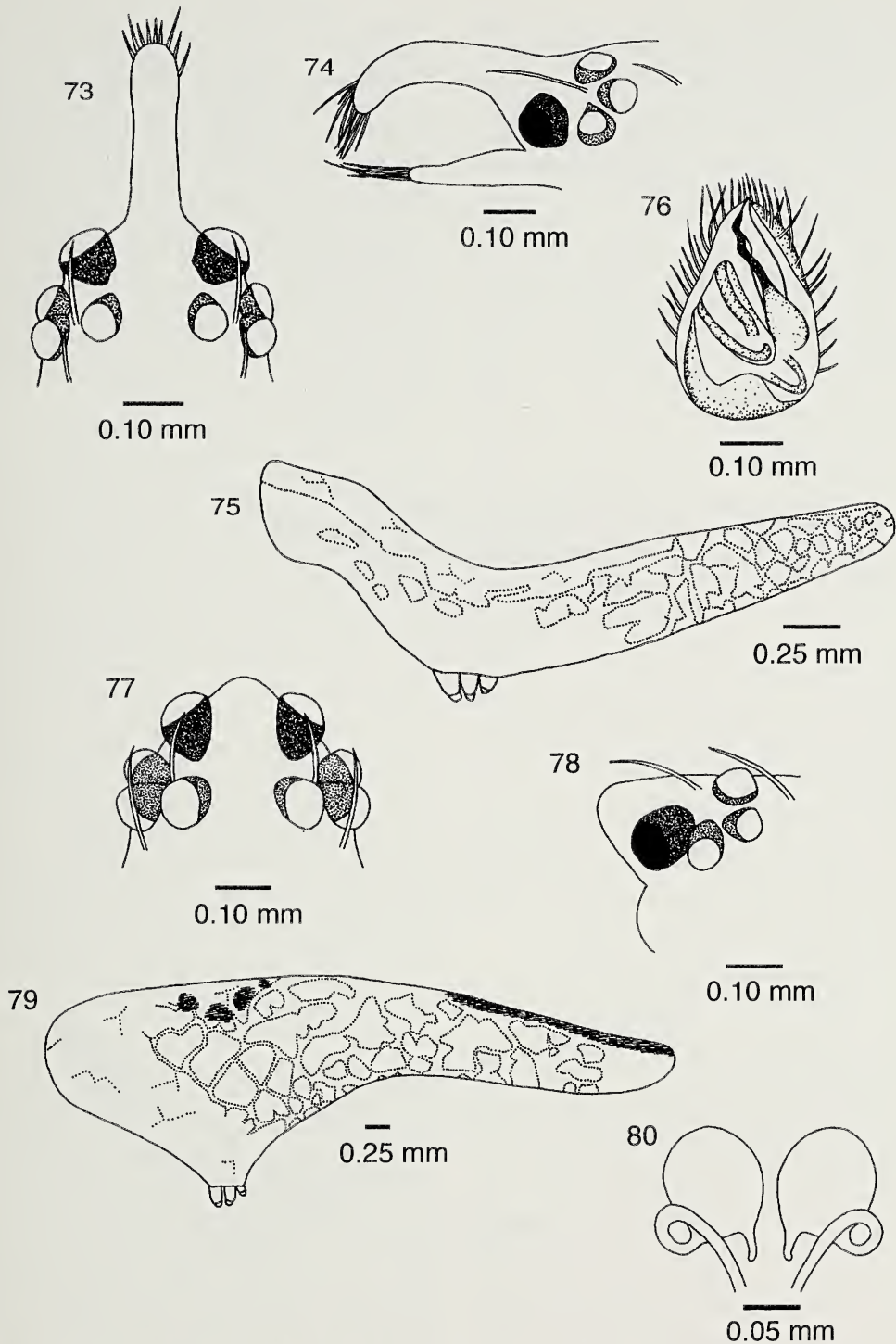
Figs. 73–80, 99, 110, 121

Type specimens.—USA: *Hawaiian Islands*: Holotype male, allotype female, Hawaii, Thurston, Hawaii Volcanoes National Park, 1067 m elev., 19.42°N, 155.23°W, 29 May 1998, M. Rivera, A. Vandergast (BPBM); 1 paratype female, Hawaii, Honomalino, 1036 m elev., 19.17°N, 155.87°W, 5 March 1999, J. Garb, K. Fay, S. Steven (EMUC).

Etymology.—The specific epithet, regarded as a noun in apposition, is from the Hawaiian word “waikula” meaning gold-colored, and refers to the solid gold color of the abdomen.

Diagnosis.—Male *Ariamnes waikula* can be distinguished based on the embolus which has very shallow undulations, bent up at tip to distal margin of cymbium, slightly shorter than the conductor (Figs. 76, 99). Cephalic process differs from *A. alepeleke* by being long and markedly curved over at distal end (Fig. 74). In females, copulatory ducts a simple loop (Fig. 80). In both sexes the entire abdomen is covered with large silver blocks with red superimposed on top.

Description.—*Holotype male* (Figs. 73–76, 99): Carapace pale with dark lines running down either side of midline. Abdomen dull brown covered all over with large irregular silver blocks, with red superimposed on top (Fig. 75). Posterior eyes separated by $2.0 \times$ diameter (Fig. 73). Cephalic process long, 19% length of carapace, curved over at distal end, not noticeably distended at tip with numerous robust setae (Fig. 74). Clypeal process 70% length of cephalic process. Abdomen relatively long, $1.3 \times$ higher at spinnerets than half way between the spinnerets and posterior



Figures 73–80.—*Ariamnes waikula* new species: 73–76, male holotype; 77–80, female allotype. 73. Cephalic process, dorsal view; 74. Cephalic and clypeal processes, lateral view; 75. Abdomen, lateral view; 76. Left palpus, ventral view; 77. Cephalic area, dorsal view; 78. Cephalic and clypeal area, lateral view; 79. Abdomen, lateral view; 80. Vulva, dorsal view.

end (Fig. 75). Abdomen 3.2 mm length, 60% of this posterior to spinnerets. Carapace 1.8 mm. Palp (Figs. 76, 99): embolus with very shallow undulations, bent up at tip, terminating at distal margin of cymbium; conductor (membranous) narrowing towards tip and terminating just above distal edge of cymbium, slightly longer than embolus.

Allotype female (Figs. 77–80, 110, 121): Color similar to male. Posterior eyes separated by $1.9 \times$ diameter (Fig. 77). Cephalic process 5% length of carapace, slightly more pointed and larger ($5.0 \times$ as long) than clypeal process (Fig. 78). Abdomen elongate, $\sim 2.3 \times$ higher at spinnerets than half way between the spinnerets and posterior end (Fig. 79). Abdomen 6.6 mm length, 69% of this posterior to spinnerets. Carapace 1.8 mm length, 1.0 mm width. Vulva (Fig. 80): receptacles spherical, ducts with single tight loop. In external view, receptacles and ducts clearly visible (Fig. 110), scape short and slightly curved (Fig. 121).

Variation.—Total length 4.8–5.0 mm in males, 8.0–9.3 mm in females, due to variable elongation in the abdomen. The abdomen is shiny, iridescent gold in life, sometimes with red marks.

Natural history.—*Ariamnes waikula* is found in wet forest habitats at middle elevations on Hawaii island. It lives under larger leaves in the forest, and to date has been found to be exclusively free-living.

Ariamnes hiwa new species

Figs. 81–88, 100, 111, 122

Type specimens.—USA: *Hawaiian Islands*: holotype male, Hawaii, Thurston, Hawaii Volcanoes National Park, 1067 m elev., 19.42°N, 155.23°W, 29 May 1998, M. Rivera, A. Vandergast (BPBM); allotype female, Hawaii, Puu Makaala, 1067 m elev., 19.55°N, 155.22°W, October 1997, D. Preston (BPBM); 1 paratype female, Hawaii, Puna Forest Reserve, 640 m elev., 19.44°N, 155.03°W, 11–14 February 1983, Y. Ching, S. Gon III (BPBM); 1 paratype male, 1 paratype female, Hawaii, Thurston, Hawaii Volcanoes National Park, 1067 m elev., 19.42°N, 155.23°W, 29 May 1998, M. Rivera, A. Vandergast (EMUC).

Etymology.—The specific epithet, regarded as a noun in apposition, is from the Hawaiian word “hiwa” meaning black and refers to the

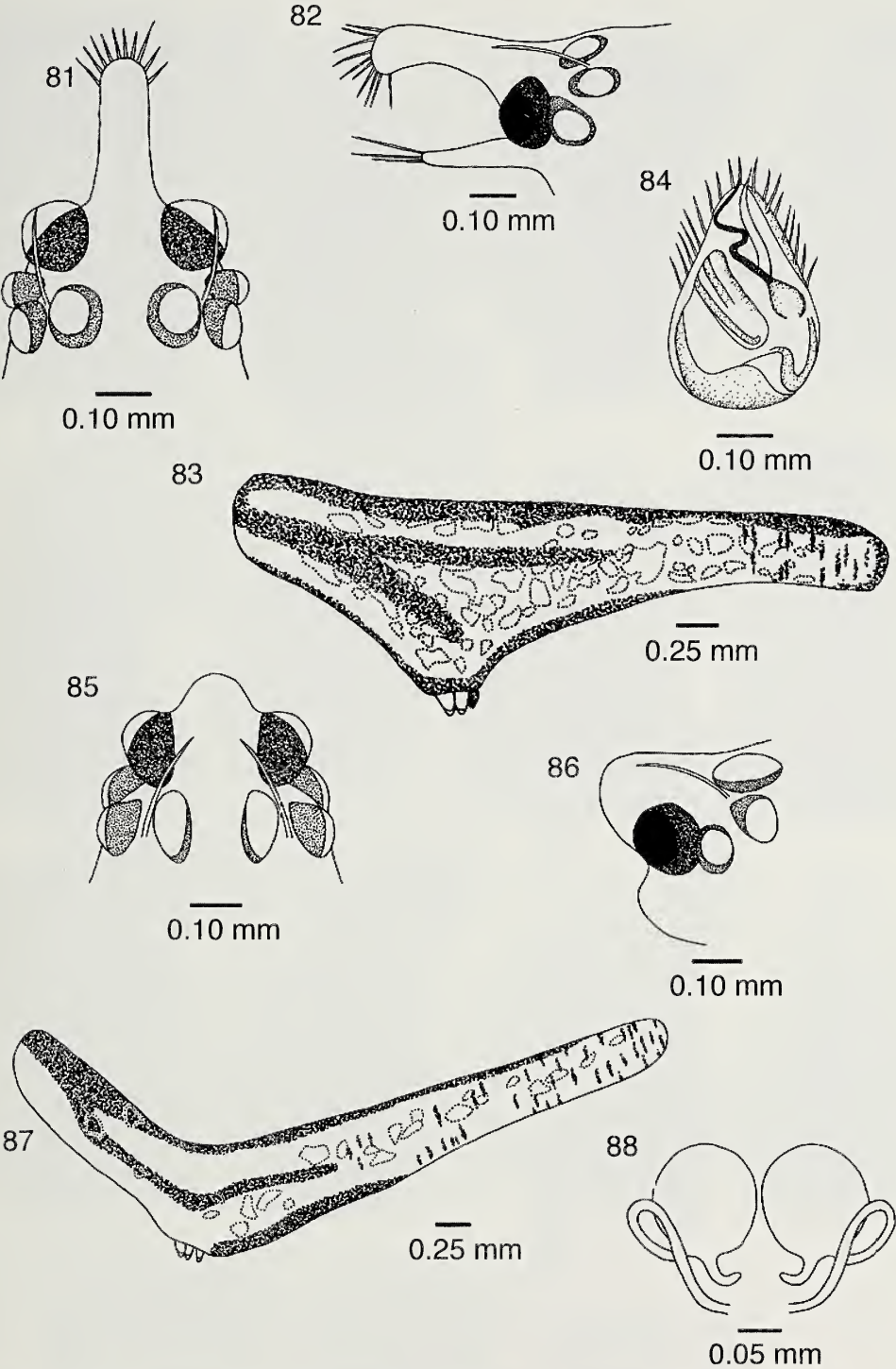
black dorsal surface of the abdomen of these spiders.

Diagnosis.—Male *Ariamnes hiwa* can be distinguished based on the embolus which has a deep distal undulation, coupled with long conductor drawn out into thread-like tip extending beyond distal margin of cymbium, much longer than conductor (Figs. 84, 100). Cephalic process very slightly curved over and distended at distal end (Fig. 82). In females, copulatory ducts in open figure-eight (Fig. 88). In both sexes the entire abdomen is dark black/brown on top, abdomen greatly elongated beyond spinnerets.

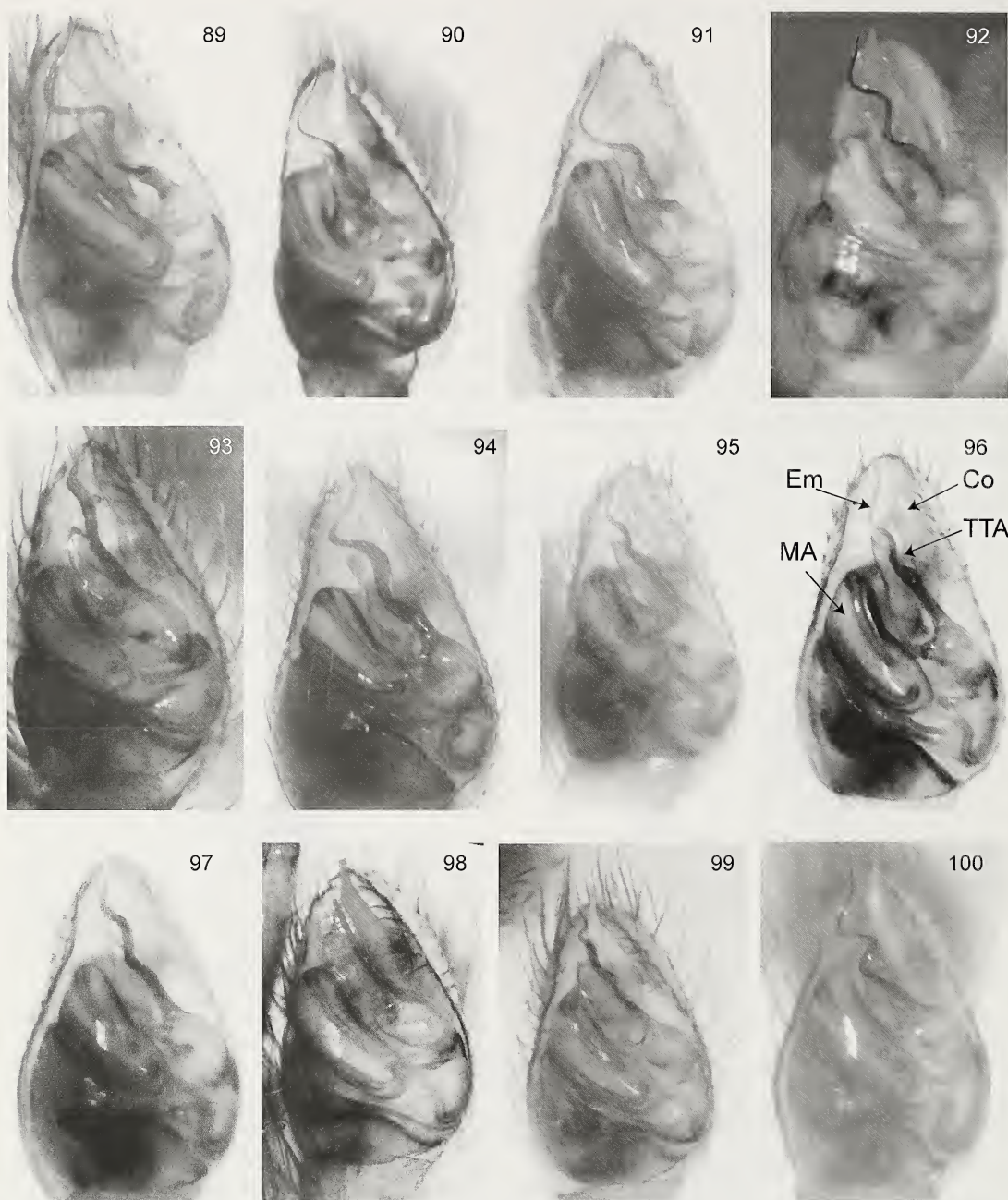
Description.—*Holotype male* (Figs. 81–84, 100): Carapace dark, lighter band running down midline. Abdomen dark on dorsal surface, brown below with scattered silver blocks and black flecks (Fig. 83). Posterior eyes separated by $1.1 \times$ diameter (Fig. 81). Cephalic process 15% length of carapace, curved over very slightly and somewhat distended at distal end with numerous robust setae (Fig. 82). Clypeal process 70% length of cephalic process. Abdomen relatively long, $2.1 \times$ higher at spinnerets than half way between the spinnerets and posterior end (Fig. 83). Abdomen 4.0 mm length, 63% of this posterior to spinnerets. Carapace 1.9 mm length, 0.9 mm width. Palp (Fig. 84, 100): embolus with very deep distal undulation, terminating just above distal margin of cymbium; conductor (membranous) narrowing distally and drawn out into long thread-like extension, extending well above distal margin of cymbium.

Allotype female (Figs. 85–88, 111, 122): Color similar to male. Posterior eyes separated by $1.4 \times$ diameter (Fig. 85). Cephalic process 5% length of carapace, similar in shape and larger ($3.7 \times$ as long) than clypeal process (Fig. 86). Abdomen elongate, only $\sim 1.5 \times$ higher at spinnerets than half way between the spinnerets and posterior end (Fig. 87). Abdomen 5.2 mm length, 66% of this posterior to spinnerets. Carapace 1.9 mm length, 0.9 mm width. Vulva (Fig. 88): receptacles spherical, ducts coiled in open figure-eight. In external view, upper portion of receptacles distinct, making them appear semicircular in shape, epigynal area indistinct (Fig. 111), scape tightly hooked (Fig. 122).

Variation.—Total length varies 5.2–5.9



Figures 81–88.—*Ariamnes hiwa* new species: 81–84, male holotype; 85–88, female allotype. 81. Cephalic process, dorsal view; 82. Cephalic and clypeal processes, lateral view; 83. Abdomen, lateral view; 84. Left palpus, ventral view; 85. Cephalic area, dorsal view; 86. Cephalic and clypeal area, lateral view; 87. Abdomen, lateral view; 88. Vulva, dorsal view.

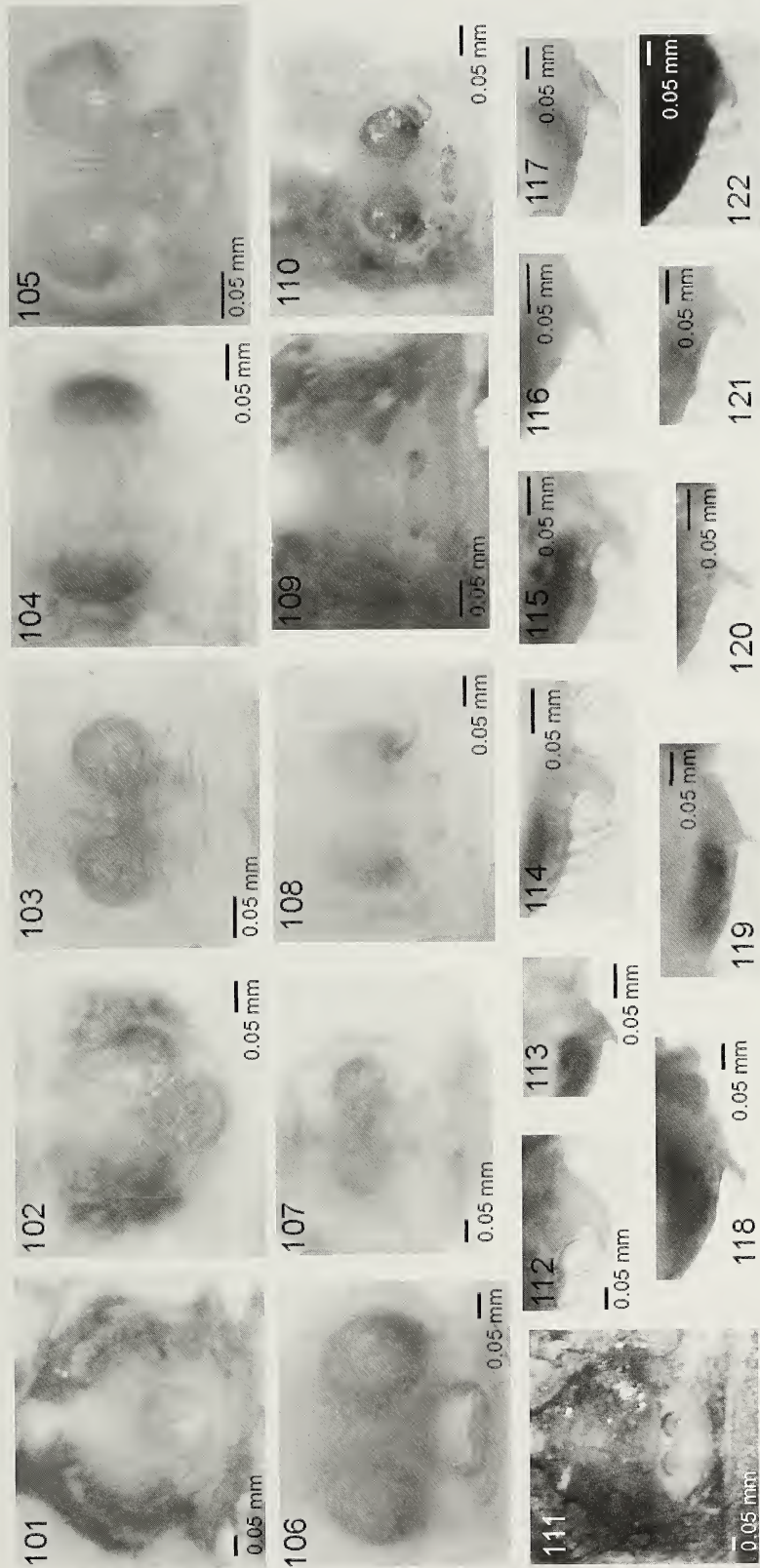


Figures 89–100.—High magnification photographs of male *Ariamnes* palps in ventral view: 89. *Ariamnes kahili*; 90. *A. huinakolu*; 91. *A. makue*; 92. *A. uwepa*; 93. *A. poele*; 94. *A. melekalikimaka*; 95. *A. corniger* E. Maui, north slope; 96. *A. corniger* E. Maui, south slope; 97. *A. alepeleke*; 98. *A. laau*; 99. *A. waikula*; 100. *A. hiwa*. Em = embolus, Co = conductor, TTA = theridiid tegular apophysis, MA = median apophysis.

mm in males, 7.0–7.4 mm in females. The abdomen is very darkly colored with little apparent variability.

Natural history.—*Ariamnes hiwa* is found

in wet forest habitats at middle elevations on Hawaii island. This species is very dark in color, and has been collected exclusively in the free-living state, where it appears to occur



Figures 101–122.—High magnification photographs of *Ariamnes* vulvas: 101–111, ventral views; 112–122, lateral views. 101. *A. kahili*; 102. *A. huinakolu*; 103. *A. makue*; 104. *A. uwepa*; 105. *A. poele*; 106. *A. melekalkimaka*; 107. *A. corniger*; 108. *A. alepeleke*; 109. *A. laau*; 110. *A. waikula*; 111. *A. hiwa*; 112. *A. kahili*; 113. *A. huinakolu*; 114. *A. makue*; 115. *A. uwepa*; 116. *A. poele*; 117. *A. melekalkimaka*; 118. *A. corniger*; 119. *A. alepeleke*; 120. *A. laau*; 121. *A. waikula*; 122. *A. hiwa*.

low down near the ground, often in rocky sites and inside rocky crevices.

ACKNOWLEDGMENTS

We are grateful to the following for help in collecting specimens: Miquel Arnedo, Adam Asquith, Andy Bohonak, Curtis Ewing, Gustavo Hormiga, Jim Liebherr, Art Medeiros, David Preston, Alfred (Alepeleke) Rivera, George Roderick, AnMing Tan, Kerry Shaw, Karen Teramura, Bonnie Thorsby, and Amy Vandergast. Thanks also to the Muséum National d'Histoire Naturelle, in particular Christine Rollard, and the Bishop Museum, in particular Neal Evenhuis and Tino Gonsalves, for assistance in obtaining specimens. We are grateful to the following organizations for providing access to collection localities: State of Hawaii Department of Land and Natural Resources (especially Betsy Gagné and John Giffin), The Nature Conservancy of Hawaii, West Maui Land and Pineapple (especially Randy Bartlett), Haleakala National Park (especially Art Medeiros and Lloyd Loope) and Hawaii Volcanoes National Park. We owe much thanks to Jennifer Kane for help with the illustrations. This work has been supported by funds from the NSF and the Schlinger Foundation (to RGG) and from the Ecology, Evolution, and Conservation Biology Program and the Haumana Graduate Program at the University of Hawaii at Manoa (to MAJR).

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SEISMIC SEXUAL SIGNAL DESIGN OF TWO SYMPATRIC BURROWING TARANTULA SPIDERS FROM MEADOWS OF URUGUAY: *EUPALAESTRUS WEIJENBERGHI* AND *ACANTHOSCURRIA SUINA* (ARANEAE, THERAPHOSIDAE)

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ABSTRACT. *Eupalestrus weijenberghi* (Thorell 1894) and *Acanthoscurria suina* Pocock 1903 are two fossorial, sympatric, synchronic, and similar-sized species of tarantulas that inhabit the meadows of Uruguay. Both species use seismic signals for communicating during courtship (body vibrations in males, leg tapping in females), but little is known either about temporal and spectral signal characteristics or effective signal range. Males were elicited to court (body vibrations) by exposing them to sexual pheromones in one end of a terrarium, whereas females were successively placed in burrows at different distances from the courting male. Seismic male signals were registered by using a geophone placed near the females. We found that *E. weijenberghi* male signals reach at least 135.75 cm, whereas *A. suina* signals reach at least 110.5 cm. There was no correlation between latency of female response and distances at which the male was courting for either of the spider species. For *A. suina*, a bout of vibration was characterized by two syllables (tucks), followed by a series of syllables (buzz 1 and buzz 2). *Eupalestrus weijenberghi* males show several tucks, followed by buzz 1 and buzz 2. Differences in sexual signals (length of syllables and number of tucks) are assumed to maintain the reproductive isolation between these similar sized, sympatric and synchronic species. Similarities are seen in adaptations to the same environment, allowing effective rates of sexual communication at long distances.

Keywords: Tarantula male signals, seismic signal reach, courtship behavior

Vibratory sexual signals (acoustic and seismic) are frequently used by courting male spiders, including tarantulas (Uetz & Stratton 1982, 1983; Prentice 1992, 1997; Quirici & Costa 2005). As tarantulas are nearly blind, vibratory signals are particularly useful as these signals do not need light to be perceived and they are quite directional (Foelix 1982; Redondo 1994). Long distance communication is particularly important for male spiders due to the cannibalistic lifestyle of females (Krafft 1980; Uetz & Stratton 1983), and, as mentioned by Narins (1990) and by Endler (2000), these signals propagate long distances without loss of effectiveness. Seismic signals generated by male spiders can reach 1 m in ctenids (through leaves, Rovner & Barth

1981; Barth et al. 1988) and 1.20 m in theraphosids (using an artificial substrate Prentice 1997). The usual indicator of effective signals is the behavioral change of the receptive female. The most unambiguous receptive response is a female signal, usually leg waving, leg tapping, or body vibrations. These behaviors have been observed in lycosids (Rovner 1968; Costa 1975), ctenids (Rovner & Barth 1981) and theraphosids (Prentice 1992; Quirici & Costa 2005).

Eupalestrus weijenberghi (Thorell 1894) and *Acanthoscurria suina* Pocock 1903 are two sympatric, synchronic, and similar-sized tarantulas species that inhabit burrows in the meadows of Uruguay. Both species can be found in high densities: *E. weijenberghi* shows a random distribution while *A. suina* shows aggregated distribution (Pérez-Miles et al. 2005). The mating season of these two species is brief and synchronic, starting at the end of the summer (February–March) when a huge number of walking males appear on the

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roads (“road tarantulas”) and ending two month later when all males die (Costa & Pérez-Miles 2002; Pérez-Miles et al. 2005). Adult males live only 2 mo in the wild, but persist in good body condition for 4–5 mo under laboratory conditions (Pérez-Miles et al. 2005); females can live around 8–10 yr (Costa pers. obs.). Females continue molting throughout their lives, so in each molt they become “virgins” (without sperm in the sperm receptacles).

These two species share the same reproductive strategy and behavior. They can be distinguished by color (*A. suina* brown, *E. weijenberghi* black, with pale bands in legs), by conspicuous tibial spurs (only on *E. weijenberghi* forelegs), and by defensive displays (*A. suina* raises forelegs and opens fangs, whereas *E. weijenberghi* raises the abdomen). When the walking male touches the female silk, which has been imbued with sexual pheromone, he courts the female primarily by means of body vibration. Body vibrations generate seismic signals eliciting receptive female behavior (leg tapping), which orients the male toward the burrow entrance (Quirici & Costa 2005). The seismic nature of this system was elucidated by Quirici & Costa (2005) using a discontinuous substrate, but effective signal range and details of their temporal and spectral characteristics were unknown. Our objectives in the present study were to find out the temporal characteristics of the signals of both species, and also to find out how far signals propagate and still elicit female leg tapping displays.

METHODS

Materials.—Spider males of both species were collected during March 2004 in the provinces of Canelones (Solymar Norte, 34°45'S, 56°00'W, and Salinas Norte, 34°45'S, 55°50'W) and Montevideo (Melilla, 34°45'S, 56°20'W), Uruguay, with the maximal distance among captures being 40 km. For all experiments, females of known reproductive history were used. They were collected from the same localities between 1996 and 1999 and raised under laboratory conditions. All females used in the study molted in the laboratory between December 2003 and January 2004. A total of 10 females and 25 males for each species were used in this study. They were housed in glass jars of 9.5 cm diameter



Figure 1.—Schematic representation of the experimental design used for the two theraphosid species. Broken vertical lines represent the metallic grid separating the male from the female. Males were placed on the soil, in the same place, while females remained inside the burrows that were chosen by us at random.

and 15 cm height, with 5 cm of soil as substrate and water provision, and were fed live cockroaches (*Blaptica dubia*, *Blattaria*, *Blaberidae*) provided ad libitum. Voucher specimens of both species were deposited in the entomological collection at the School of Sciences, Universidad de la República, Montevideo, Uruguay.

Spiders were kept in captivity for at least two weeks before being tested. Experiments were carried out in four long glass terraria of 20 cm width and 20 cm height containing a 7 cm thick layer of soil as a substrate (collected from their natural habitat). For *E. weijenberghi*, the length of the two terraria used was 170 cm; for *A. suina*, the two terraria measured 120 cm length because preliminary observations had suggested that *E. weijenberghi* signals reached farther than those of *A. suina*. In each terrarium, five burrows were constructed in a line against the glass wall, allowing visual observations of female behavior inside burrows. The distance between two consecutive burrows was 30 cm for *E. weijenberghi* and 25 cm for *A. suina* (Fig. 1). Each terrarium was placed on an anti-vibratory table (weighty wood plate placed on four inflated bicycle tires) in order to minimize ground vibrations and to prevent seismic signals from passing between terraria (in a preliminary study without the anti-vibratory table a female responded to a courting male in an adjacent terrarium). A geophone with vertical polarization (Geospace industries, model GS 20-DX, damping resistor = 1000 ohms) was used to collect substratum-coupled vibratory signals. To test if signals would pass to an adjacent terrarium, the geophone was placed in one terrarium and a courting male in the

Table 1.—Experimental design for each of the four terraria used in this study (two for *A. suina* and two for *E. weijenberghi*). Each male group was composed of five individuals, and each of them was used once with one female for each of the two terraria. The five females (A, B, C, D, and E) were located in each burrow, avoiding repeated encounters with the same male. A total of 50 trials were performed for each spider species.

	Burrow	Burrow	Burrow	Burrow	Burrow
Males	1	2	3	4	5
Group 1	A	B	C	D	E
Group 2	E	A	B	C	D
Group 3	D	E	A	B	C
Group 4	C	D	E	A	B
Group 5	B	C	D	E	A

other, and any courting signals could be registered by the geophone. Data were recorded on an analog recorder UHER 4200, at a speed of 9.5 m/s (frequency band of 20 Hz to 16 kHz). Experiments were carried out from 16 March to 16 April 2004, synchronously with the reproductive period of these species under natural conditions. During the experiments, mean room temperature was 24.96° C (± 2.05 SD).

Experimental design.—Preliminary experiments analyzing the duration of bouts of vibrations produced by males prompted the use of the two step sample method in this study (Snedecor & Cochran 1984). Primary sample units were the species and the secondary samples units were the individuals within each species. Variance components were examined throughout one-sample two-step ANOVA (hierarchical ANOVA), following Sokal & Rohlf (1979). The experimental design is shown in Table 1. The order of consecutive burrows, where females were located one a time, is indicated in Arabic numbers (1 to 5). Individual females are identified by capital letters (A to E). All burrows were tested with a female inside, perceiving male vibration bouts at all the experimental distances. Each group (1 to 5) was composed of five different males. All the males used, as well as the male-female pairs and the female burrow locations, were randomly assigned but repetition was avoided. Since two terraria were used for each species, each male courted two different females during the entire experimental period, one in each terrarium. Consequently, each female was ex-

posed to two different males. Only one experiment was conducted per day.

Trials in each terrarium were carried out for ≥ 24 h, allowing each female to adapt to the burrow (acclimatization period). This time period also allowed another female to release sex pheromones at the end of the terrarium where the males were located to help elicit male courtship. At approximately 19:00 h this last female was removed and a male was located in the same place. The time of each experiment was recorded from the start of male courtship until completion of female sexual response or until 30 min after courtship if there was no female response. The geophone was located each time near the entrance of the occupied burrow. Distance from males to the geophone vary from 21.5 cm, 50.5 cm, 75.5 cm, 110 cm and 134.75 cm for *E. weijenberghi*, and 15.25 cm, 37.25 cm, 60.25 cm, 84.75 and 110.5 cm for *A. suina*, which correspond to the burrow location. A total of 50 trials was recorded for each species.

Data analysis.—The temporal characteristics of male courtship signals were analyzed using the software, Sound Ruler (0.9.4.0), which allows the visual and acoustic identification of pulses and accompanying silences. We analyzed a total of 47 male courtship signals for *E. weijenberghi* and 67 for *A. suina*, belonging to 15 males from each species.

The Fisher two tailed exact probability test (Siegel 1956) was used to compare the occurrence of female response among burrows for each species. The latency of female response was used as an estimate of female receptivity (defined as the time period from the end of the first male bout of vibration until the first female leg tapping, according to Quirici & Costa 2005). Simple linear regression was used to examine a relationship between the latency of female response (dependent variable) and the distance between male and female (as an independent variable). Previously, regression analysis residues were plotted in order to remove outliers and assess normality. Analyses of variance were used for testing significance of the regressions (Daniels 1989).

When assumptions of normality or variance homogeneity were not confirmed, non-parametric tests (Mann-Whitney U-test and Kruskal-Wallis) were used. All statistical analyses were performed using the software program, Rproject (<http://www.r-project.org>).

Table 2.—Occurrence frequency of leg tapping from 10 different females located in the five burrows. Distances between vibrating male and each female burrow were: 1 = 21.5 cm, 2 = 50.5 cm, 3 = 75.5 cm, 4 = 110 cm and 5 = 134.75 cm for *E. weijenberghi*, and 1 = 15.25 cm, 2 = 37.25 cm, 3 = 60.25 cm, 4 = 84.75 and 5 = 110.5 cm for *A. suina*.

	Burrow				
	1	2	3	4	5
<i>E. weijenberghi</i>	10	9	10	9	9
<i>A. suina</i>	8	8	6	7	8

RESULTS

Female responses.—In 94% of the trials with *E. weijenberghi* and 74% of the trials with in *A. suina*, females responded to courtship at all distances, including cases at the maximal possible distance for *E. weijenberghi* (135.75 cm) and also for *A. suina* (110.5 cm) (Table 2). No statistical differences were found using the Fisher exact test when comparing the occurrence of female response of each species in each of the five burrows ($P = 0.474$ for burrow 1, $P = 1$ for burrow 2, $P = 0.086$ for burrow 3, $P = 0.582$ for burrow 4, and $P = 1$ for burrow 5).

Table 3 shows the recorded values of latency of female calls for both species and for each burrow. The latency was highly variable in both species, with all the obtained variation coefficients higher than 60%. When comparing latency values across all five burrows, we found no statistical differences either for *E. weijenberghi* ($H_{4,47} = 1.192$, $P = 0.879$) or for *A. suina* ($H_{4,37} = 1.032$, $P = 0.905$).

Simple linear regression analyses showed no significant correlation between distance and latency of female response, neither for *E.*

weijenberghi ($F_{[calculated]} = 0.479$, $F_{[critical]} = 0.492$, $n = 44$, $P = 0.09$) nor for *A. suina* ($F_{[calculated]} = 0.257$, $F_{[critical]} = 0.614$, $n = 35$, $P = 0.37$). Moreover, distance explained less than 2% of variation in female behavior in both species.

***Acanthoscurria suina*: description of male courtship signal.**—The set of consecutive male body vibrations separated by pauses, or “bouts,” was characterized by two temporal components. A first component included a single syllable, identified as “tuck,” whereas a second component involved a series of syllables, referred to as “buzzes” (terms were chosen to resemble the sounds made by the spiders) (Fig. 2). A typical male vibration bout was composed of two consecutive “tucks” (tuck 1 mean duration = 0.100 s, SD = 0.113, $n = 22$; tuck 2 mean duration = 0.064 s, SD = 0.025, $n = 25$) followed by two consecutive “buzzes.” (buzz 1 mean duration = 0.55 s, SD = 0.34, $n = 63$; buzz 2 mean duration = 0.745 s, SD = 0.237, $n = 54$). Periods of silence between tucks, between tuck 2 and buzz 1 and between buzz 1 and buzz 2, were called “interpulses”: I1 (mean duration = 0.282 s, SD = 0.14, $n = 16$), I2 (mean duration = 0.414 s, SD = 0.382, $n = 24$) and I3 (mean duration = 0.589 s, SD = 0.184, $n = 52$), respectively.

There were no significant differences between the duration of tuck 1 and tuck 2 ($U = 148$, $P = 0.429$, $n = 14, 25$). When comparing all interpulse periods, significant differences were found (Kruskal-Wallis test: $H_{2,92} = 23.44$, $P < 0.001$). Interpulse 3 (I3) had the longest mean value. Buzz 2 had a greater duration than buzz 1 (two-tailed t-test, $t = -4.5$, $df = 115$, $P < 0.001$).

***Eupalaestrus weijenberghi*: description of male courtship signal.**—As in *A. suina*, male

Table 3.—Latency (s) for female response (leg tapping behavior) for both tarantula species and for each burrow. Values shown are means, standard deviations (SD) and coefficients of variation (CV).

Burrow	<i>Eupalaestrus weijenberghi</i>			<i>Acanthoscurria suina</i>		
	Mean	SD	CV	Mean	SD	CV
1	172.33	245.27	142%	246.97	188.3	76%
2	80.5	76.1	95%	321.13	468.98	146%
3	104.96	68.78	66%	366.9	236.65	65%
4	79.82	47.5	60%	456.27	518.63	114%
5	127.63	193.89	152%	288.5	311.28	108%

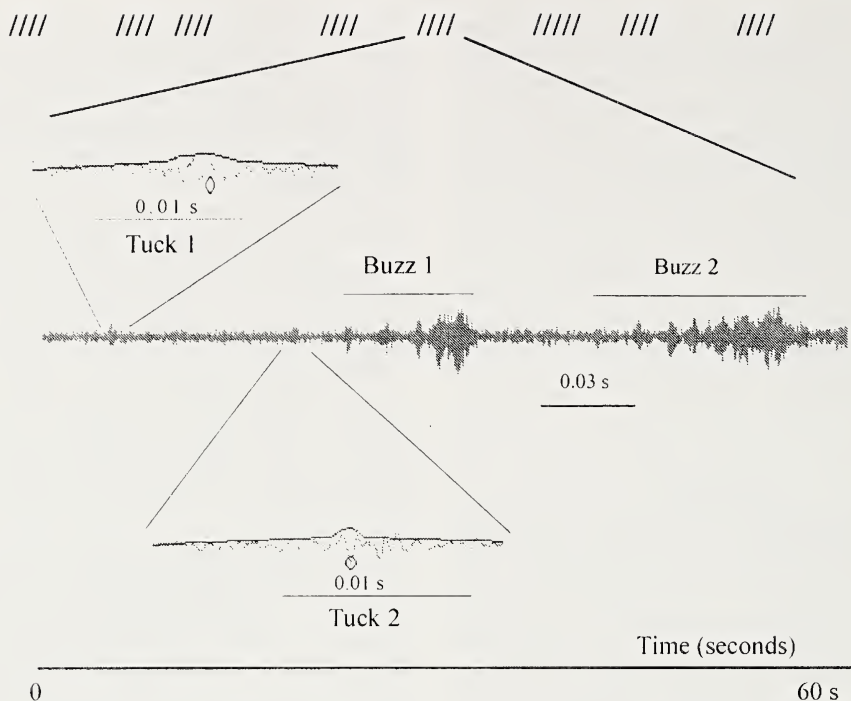


Figure 2.—Above: schematic drawing of male *A. suina* courtship through time. Oblique lines represent a “bout” of vibration produced by the male. Entire sequence corresponded to one minute. Below: oscillogram of a single bout of vibration. All the components are indicated (tucks, interpulse periods, and buzz). Tuck 1 and tuck 2 were amplified.

bout vibrations of *E. weijenberghi* presented single syllables or tucks (tuck 1 mean duration = 0.066 s, SD = 0.034, $n = 33$; tuck 2 mean duration = 0.088 s, SD = 0.049, $n = 33$) and sequences of syllables or buzzes (buzz 1 mean duration = 0.871 s, SD = 0.238, $n = 46$; buzz 2 mean duration = 0.812, SD = 0.183, $n = 45$). Separately by a series of interpulses: I1 (mean = 0.391 s, SD = 0.289, $n = 33$), I2 (mean = 0.504 s, SD = 0.3, $n = 33$) and I3 (mean = 0.459 s, SD = 0.159, $n = 45$). However, vibrations in *E. weijenberghi* differed from *A. suina* signals in the number of tucks preceding buzzes, from six to eight. Figure 3 shows a schematic representation of a male vibration bout throughout time and an oscillogram of a bout of *E. weijenberghi*.

There were no statistical differences in the duration of the tucks before buzz 1 ($U = 398.5$, $P = 0.062$, $n = 33$, 33), or among silences (Kruskal-Wallis test, $H_{2,110} = 5.92$, $P = 0.06$). Contrary to *A. suina*, no differences between buzz 1 and buzz 2 were found ($t = 1.3$, $df = 89$, $P = 0.194$).

Male sexual signal vibrations: comparing

both spider species.—When signal components were compared, buzz 1 of *E. weijenberghi* showed a longer duration than *A. suina* ($t = 7.067$, $P < 0.001$, $df = 107$), whereas interpulse duration between buzz 1 and buzz 2 was longer in *A. suina* ($t = -3.667$, $P = 0.004$). No significant differences were detected in any of the other parameters; durations of tuck 1 ($U = 339.5$, $P = 0.505$, $n = 33$, 23), interpulse ($U = 176$, $P = 0.08$, $n = 32$, 16), tuck 2 ($U = 316$, $P = 0.129$, $n = 33$, 25), interpulse ($t = 1.005$, $P = 0.319$, $df = 55$, $n = 33$, 24) and buzz 2 ($t = 1.569$, $P = 0.119$, $df = 97$, $n = 45$, 54). Considering all parameters measured, *E. weijenberghi* signal bouts were twice as long as *A. suina* ones (3.82 s versus 1.902 s) (taking into account all tucks that precede buzz 1 in *E. weijenberghi*) and were statistically significantly different (Mann-Whitney U-test $U = 175$, $P < 0.001$, $n = 46$, 67). So, differences between species were in the duration of buzz 1 and in the duration of I3 (*A. suina* showing higher values) and in the number of tucks that preceded buzz 1 in *E. weijenberghi* (from six to eight).

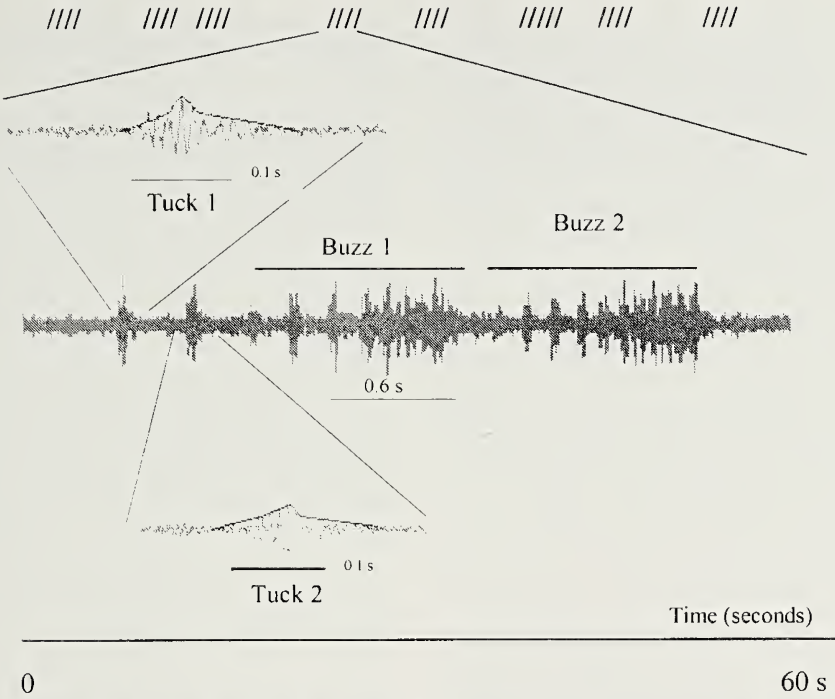


Figure 3.—Above: schematic drawing of male *E. weijenberghi* courtship through time. Oblique lines represent a “bout” of vibration produced by the male. Entire sequence corresponded to one minute. Bellow: oscillogram of a single bout of vibration. All the components are indicated (tucks, interpulse periods, and buzz). Tuck 1 and tuck 2 were amplified.

DISCUSSION

Male signal characteristics.—Since the polarization plane of the geophone was vertical, and seismic signals generated by the courting males were well perceived by the apparatus, these signals would correspond to the kind of seismic signals called “Rayleigh waves” (Narins 1990). However, the co-occurrence of signals called “Love” waves (Narins 1990) can not be discounted in *E. weijenberghi* and *A. suina*. A geophone with horizontal polarization would be required to record them and this was not available for this study. For example, the fiddler crab *Uca pugilator* use both kinds of waves for communicating (Aicher & Tautz 1990).

Three interspecific differences were found in the temporal structure of the signal: in the length of buzz 1, in the length of interpulse period between the two buzzes, and in the number of tucks that precede buzz 1. Divergence in sexual signals among sympatric and synchronous species would be an indicator that natural selection is acting on the signal design, favoring species recognition (see Dob-

zhansky 1940; Greenfield 1997). For example, the sympatric species of the ctenid spider *Cupiennius* diverge in their courtship signals, mainly in the temporal structure (Schüch & Barth 1990).

Female latency and signal efficacy.—Regression analyses showed no differences in the latency of female response as a function of male-female distances. We conclude that courtship signals were above the response threshold of females, and that signal features that elicited female responses were unchanged (until 135.75 cm in *E. weijenberghi* (135.75 cm) and 110.5 cm in *A. suina*). However field experiments would be necessary to confirm these data. For example Elías et al. (2004) found that in the salticid spider, *Habronattus dosseus* Griswold 1987 the effectiveness of male courtship seismic signal appears to be strongly constrained by the available substratum resource. Seismic signals reaching long distances were extensively reported in scorpions (Brownell & Hemmen 2001), crickets (Hill & Shadley 2001), amphibians (Lewis & Narins 1985), fossorial rodents (Heth et al.

1987, 1988; Randall 1989, 1993, 1995; Rado et al. 1989; Narins et al. 1997; Mason & Narins 2001), and spiders (Rovner & Barth 1981; Barth et al. 1988; Prentice 1997). Therefore, we can make a prediction about what could occur in open grasslands. Given that female burrows are in high densities (from 0.07 individuals/m² to 0.65 individuals/m²) with distances between burrows entrances ranges from 8.0 cm to 36 cm (Pérez-Miles et al. 2005), many females could respond to male seismic signals and compete among themselves, performing leg tapping to orient the male towards each burrow entrance. This scenario is plausible principally in *A. suina* where female burrows showed an aggregated distribution.

The use of seismic signals.—Sharing the same spatial and temporal characteristics, both species would converge towards similar seismic signal characteristics. As mentioned by Greenfield (1994), the environmental and physical conditions that determine the reproductive period would be some of the pressures that determine the sexual signal design through selection of signal efficacy. Due to the fact that *Eupalaestrus weijenberghi* and *Acanthoscurria suina* inhabit the same habitat and microhabitat, it was expected that they would use the same communicatory channel. Secondly, both species are fossorial, and as some authors have postulated (Heth et al. 1988; Hill 2001; Mason & Narins 2001), the use of this kind of signal could be due to convergence because of signal efficacy and efficiency of propagation in this subterranean environment.

On the other hand, following Greenfield (1994) and Endler (2000), the concentration of males in a brief reproductive period would be an indicator that those males take advantage of singular environmental conditions when the physical conditions for transmission and reception of signals are favorable and a huge concentration of receptive females is present. The “road tarantula” males appear in large numbers during cloudy and warm days in which the relative humidity is high (Pérez-Miles et al. 2005). Substrate properties (compaction, moistening, and humidity) determine the signal speed transmission of the signal (Narins 1990; Endler 2000). Since a humid solid is a better conductor than a dry soil (Narins 1990), we propose that males of both species have been selected to take advantage of

this meteorological condition that characterizes the reproductive period of both these species.

From this present study we conclude that there exists convergence and divergence in the temporal signal characteristics between these species and that the signals produced by males are propagated long distances. In addition males appear to be taking advantage of the climatological conditions of the reproductive period when the signals transmission efficiency is high.

ACKNOWLEDGMENTS

We are very grateful to Peter Narins who gave us the equipment to gather the data. We also thank Mario Penna for his help during the different stages of the work and for his corrections and suggestions on the first draft of the manuscript. Angel Caputi taught V.Q. to analyze signals and helped us with her suggestions. Gabriel Francescoli gave us the tape recorder and some literature. We also thank Luis Ebensperger for suggestions on the first draft of the manuscript and for improving the English. We also appreciate the constructive criticisms of two anonymous reviewers on a previous version of this manuscript.

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REDESCRIPTION OF *HOGNA COLORADENSIS* (BANKS 1894) FROM THE SOUTHWESTERN UNITED STATES (ARANEAE, LYCOSIDAE)

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ABSTRACT. *Hogna coloradensis* (Banks 1894) (Araneae, Lycosidae) is redescribed. Banks' original description from 1894 made identification difficult. Internal and external genitalia of both sexes are herein described and illustrated. The spider is found east of the Rocky Mountains from Wyoming south to Mexico. It constructs shallow, straight burrows that it sometimes closes with small rocks and debris. *Lycosa evagra* Chamberlin 1925 is synonymized with *H. coloradensis*.

Keywords: Taxonomy, wolf spider, synonymy

Currently 24 species of the genus *Hogna* Simon 1885 are listed for North America, and 11 for Mexico (Platnick 2006). Although some of these species are true representatives of the genus *Hogna* based upon morphological characters and sequence data, others will likely be placed in a new genus (or genera) and still others will likely be moved to *Rabidosia* (Dondale, pers. comm.). Nevertheless, a need exists to correctly identify those species currently placed in the genus until such time as a formal generic revision can be completed. Identification of these species is made challenging by the often poor descriptions with few or no illustrations. For example, Banks' original description of *Lycosa coloradensis* Banks 1894 made little mention of the epigynum saying only that, "The epigynum is red, it is an oblong cavity with undulate margins, from the bottom projects a capitate septum." He has only a cursory description of the male palp, and provides no illustrations of either sex. Here we present a redescription of *H. coloradensis* with genitalic illustrations for both sexes.

Illustrations were made from digital photographs taken using an Olympus U-CMAD3 digital camera mounted on an Olympus SZX12 stereomicroscope. All measurements are in millimeters. Specimens used in this study are deposited in the Museum of Com-

parative Zoology at Harvard University in Cambridge, MA (MCZ); the American Museum of Natural History in New York, NY (AMNH); the Division of Plant Industry in Gainesville, FL (DPI); New Mexico State University (NMSU); the University of Colorado in Boulder (CU); and the Denver Museum of Nature & Science (DMNS).

Abbreviations: AER = anterior eye row; PER = posterior eye row; PME = posterior median eye; PLE = posterior lateral eye. Coordinates for collection locales are provided unless there was too much uncertainty regarding the locale (particularly for some of the older records).

TAXONOMY

Family Lycosidae Sundevall 1833
Hogna Simon 1885

Type species.—*Lycosa radiata* Latreille 1819, by original designation.

Hogna coloradensis (Banks 1894)
Figs. 1–21

Lycosa coloradensis Banks 1894:50; Banks 1898: 268; Chamberlin 1908:249–251, plate XVII figs. 6, 7.

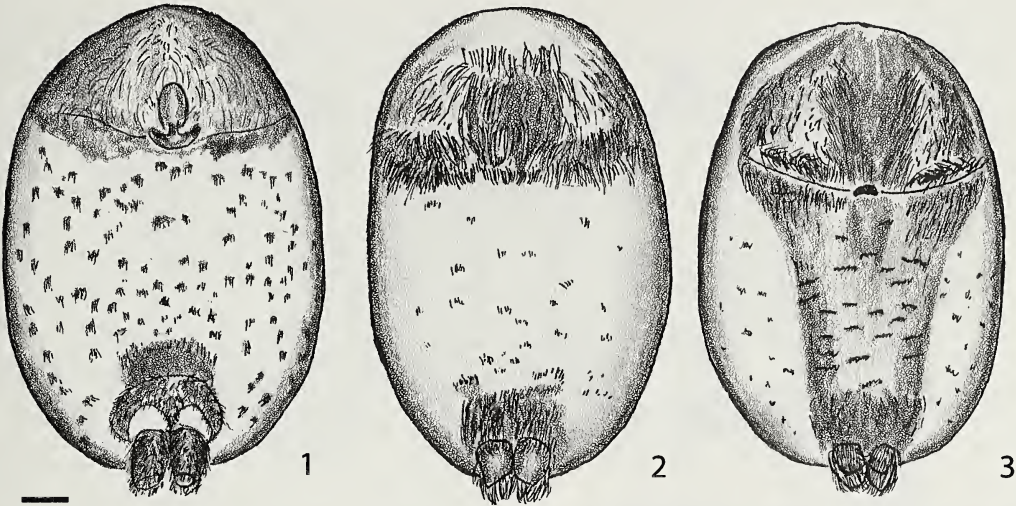
Lycosa evagra Chamberlin 1925:227. **New synonymy.**

Hogna evagra (Chamberlin 1925): Roewer 1955: 254; Platnick 2006.

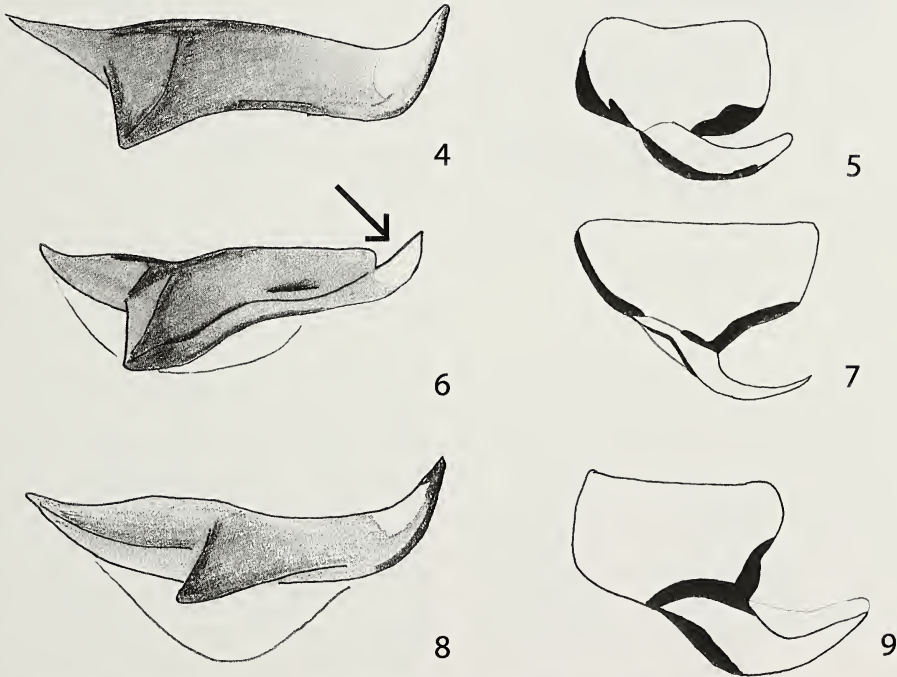
Hogna coloradensis (Banks 1894): Roewer 1955: 258; Platnick 2006.

Type material.—*Lycosa coloradensis* Banks

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Figures 1–3.—*Hogna coloradensis* venters. 1. Female from Grant County, New Mexico; 2. Male from Lordsburg, Hidalgo County, New Mexico; 3. Male from Silver City, Grant County, New Mexico. Scale line = 1 mm.



Figures 4–9.—*Hogna coloradensis* male palpal structures (prolateral views of median apophyses illustrated). 4. Median apophysis of specimen from Fort Stockton, Pecos County, Texas; 5. Terminal apophysis of Fort Stockton specimen; 6. Median apophysis of specimen from Monahans Sandhills State Park, Ward County, Texas, arrow points to area of missing membrane (see text); 7. Terminal apophysis of Monahans Sandhills State Park specimen; 8. Median apophysis of specimen from Hermosillo, Sonora, Mexico; 9. Terminal apophysis of Hermosillo specimen.

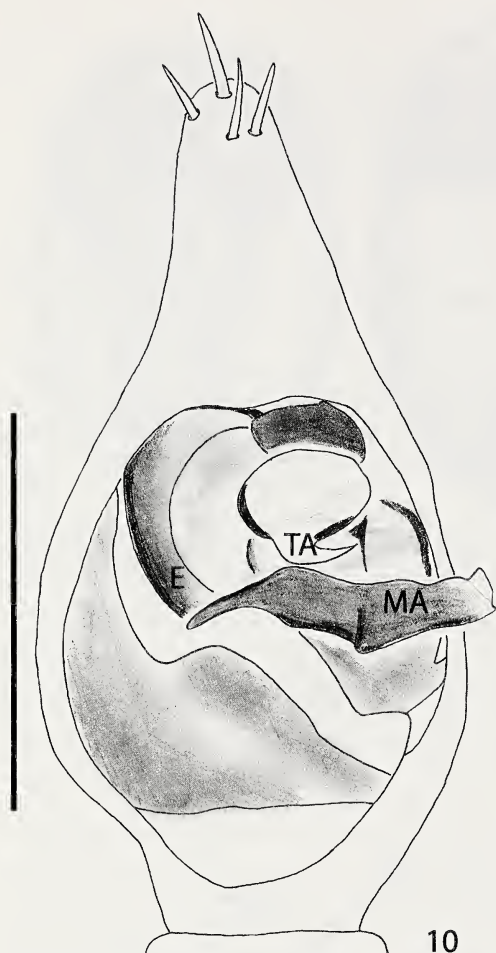


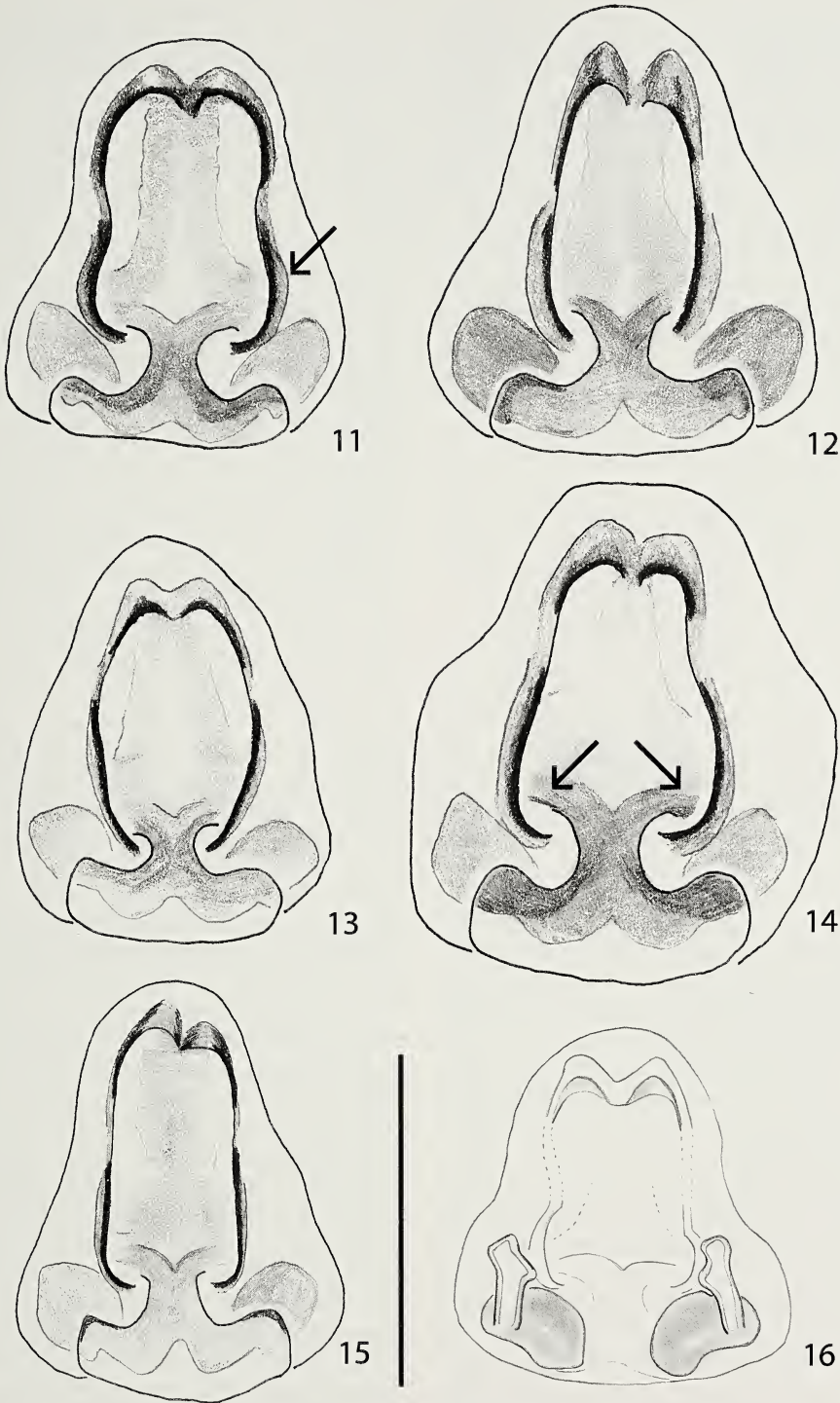
Figure 10.—Palp, ventral view, specimen from Erie, Weld County, Colorado. E = embolus (tip hidden), TA = terminal apophysis, MA = median apophysis (see text). Scale line = 1 mm.

1894: 1 syntype male, 2 syntype females: USA: Colorado: *Larimer County*, Fort Collins (40°35'N, 105°05'W, 1525 m elev.), no date, Nathan Banks collection (MCZ 20844).

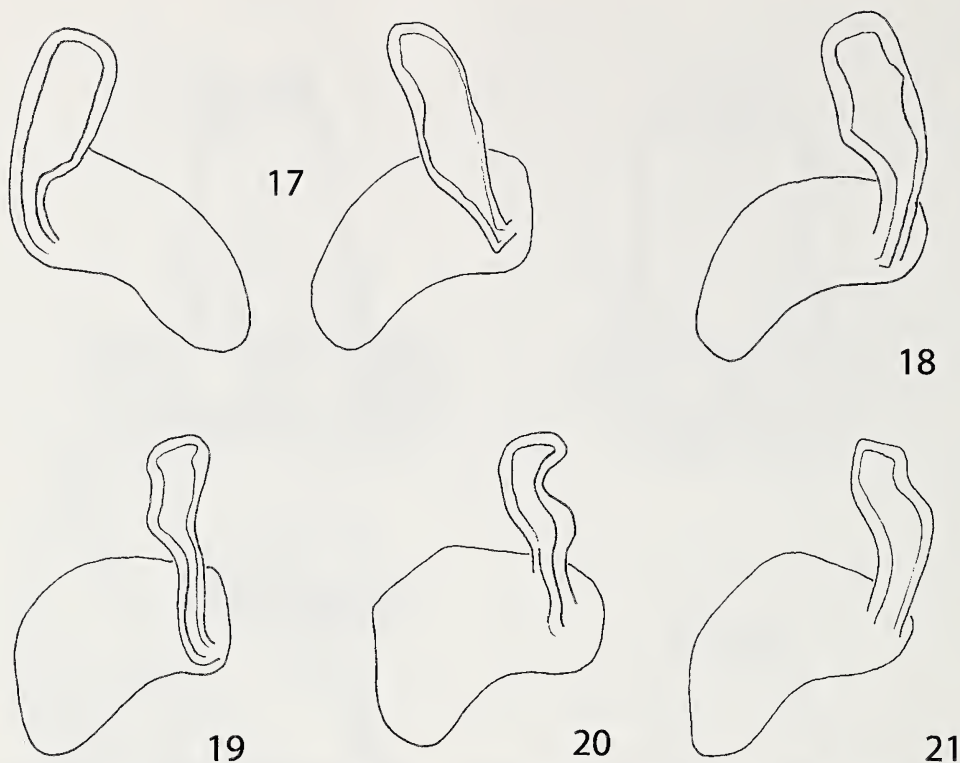
Lycosa evagra Chamberlin 1925: Holotype female: MEXICO: *Chihuahua*: Montezuma Station, exact location unknown, no date or collector (MCZ 1303).

Other material examined.—MEXICO: *Sonora*: 1 ♂, Hermosillo (29°04'N, 110°58'W), no date (MCZ 65765); USA: *Arizona*: Cochise County: 1 ♂, 1 ♀, 9.6 km E. of Portal, 1 June 1955 (CU), 1 ♂, 1 ♀, 9 June 1962 (DMNS ZA.2270); 1 ♂, 1 ♀, Portal (31°54'N, 109°08'W), 9 July 1970 (DMNS ZA.362); 1 ♂, SE. of Portal, 25 June 1970

(DMNS ZA.325); *Colorado*: Denver County: 1 ♂, Denver (39°44'N, 104°59'W), 4 February 1939 (CU); 1 ♀, Smokey Hill, 5 July 1938 (CU); Las Animas County: 1 ♀, near Chacacac Creek (37°33'N, 103°38'W), 12 June 1962 (CU); Otero County: 1 ♀, Comanche National Grasslands (39°29'N, 105°16'W), 29 May 2004 (DMNS ZA.7554); Pueblo County: 1 ♂, Pueblo West (38°18'N, 104°46'W), 25 September 1999 (DMNS ZA.9841); Weld County: 1 ♀, 20.9 km N. of New Raymer, 3 July 1962 (CU), 1 ♀, 3 July 1962 (CU); 1 ♂, 1291 County Rd. 11, Erie (40°01'N, 104°57'W), 7 October 1999 (DMNS ZA.9840), 1 ♀, Bones Galore, Pawnee National Grasslands (40°43'N, 103°48'W), 9 June 1999 (DMNS ZA.9839), 1 ♀, 10 June 1999 (DMNS ZA.9842); *New Mexico*: Dona Ana County: 1 ♂, Jornada IBP grassland site (32°36'N, 106°44'W), 26 April–3 May 1997 (NMSU); 3 ♂, 2 ♀, Jornada Range, 2.7 km S. of South Well, 1 April 1990 (NMSU); 4 ♂, 1 ♀, Jornada Range, 12 km WNW. of South Well, June 1989 (NMSU); 1 ♂, Jornada Range, Plot 1, 18–19 April 2000; 1 ♂, Everhart Ranch, Gap Tank, S. of Hotch (31°53'N, 107°03'W), 19 May 1977 (NMSU); Grant County: 1 ♀, Hurley (32°41'N, 108°07'W), 2 August 1973 (DPI), 1 ♀, 16 May 1972 (DPI), 1 ♂, 1 June 1972 (DPI), 2 ♀, 16 July 1972 (DPI), 1 ♀, 14 August 1972 (DPI), 1 ♀, 1 September 1972 (DPI), 1 ♂, 16 May 1973 (DPI), 8 ♂, 16 June 1973 (DPI), 6 ♂, 30 June 1973 (DPI), 1 ♂, 1 July 1973 (DPI), 4 ♂, 17 July 1973 (DPI), 1 ♀, 16 September 1973 (DPI); 1 ♀, Silver City (32°46'N, 108°16'W), 15 August 1972 (DPI), 3 ♂, 31 May 1973 (DPI); Hidalgo County: 1 ♂, Antelope Wells, U Bar Ranch (31°20'N, 108°30'W), 30 June 1977 (DPI); 1 ♂, Big Hatchet Ranch (31°42'N, 108°25'W), 22 June 1977 (DPI); 1 ♂, Campbell Well, Huecos Mountains (31°27'N, 108°13'W), 13 July 1977 (DPI); 1 ♂ Doyle Line Camp, 20 June 1977 (DPI); 1 ♂, Doyle Tank, Sierra Rica Mountains, 9 June 1977 (DPI); 1 ♀, Lordsburg (32°21'N, 108°42'W), 16 July 1972 (DPI), 2 ♂, 15 May 1972 (DPI), 1 ♂, 1 June 1972 (DPI), 5 ♂, 30 June 1972 (DPI), 1 ♂, 14 July 1972 (DPI), 1 ♂, 2 ♀, 16 July 1972 (DPI), 4 ♂, 15 May 1973 (DPI), 2 ♂, 31 May 1973 (DPI), 2 ♂, 29 June 1973 (DPI); 2 ♂, Stone Cabin (31°24'N, 108°17'W), 31 May 1977 (CU); Lea County: 1 ♀, 17.7 km N. of Tatum, 26 June 1991 (NMSU); San Miguel



Figures 11–16.—*Hogna coloradensis* epigyna. 11–15. Ventral view, 16. Dorsal view; 11. Syntype, Fort Collins, Larimer County, Colorado, arrow points to undulation along posterior-lateral edge of atrium (see text); 12. Specimen from Chihuahua, Mexico; 13. Specimen from Silver City, Grant County, New Mexico; 14. Specimen from Hurley, Grant County, New Mexico, arrows point to expansion of median septum (see text); 15. Specimen from Jornada Range, Dona Ana County, New Mexico; 16. Specimen from Comanche National Grasslands, Otero County, Colorado. Scale lines = 1 mm.



Figures 17-21.—*Hogna coloradensis* female spermathecae dorsal views. 17. Pair of spermathecae of specimen from Monahans Sandhills State Park, Ward County, Texas; 18. Another specimen from Monahans Sandhills State Park, Ward County, Texas; 19. Specimen from Portal, Cochise County, Arizona; 20. Specimen from Chihuahua, Mexico; 21. Specimen from Portal, Cochise County, Arizona.

County: 1 ♂, Gallinas River, Las Vegas (35°34'N, 105°12'W), 11 June 1949 (MCZ 65766); Santa Fe County: 1 ♀, SW. of Santa Fe (35°41'N, 105°56'W), 24 April 1977 (MCZ 65767); Texas: Pecos County: 1 ♂, 1 ♀, Fort Stockton (30°53'N, 102°52'W), 9 July 1974 (AMNH); Ward County, 3 ♂, 2 ♀, Monahans Sandhills State Park (31°38'N, 102°49'W), 9 July 1974 (AMNH).

Diagnosis.—*Hogna coloradensis* can be separated from all other *Hogna* and Lycosidae by a dark area immediately anterior to the epigastric furrow as well as a small dark area just anterior to the spinnerets, the rest of the venter is light with spots (Fig. 1). Although this color pattern was seen in 94% of the specimens examined, the remainder of the specimens showed some variability (Figs. 2, 3; we describe this variability below). Males can be identified by the sharply upturned prolateral end of the median apophysis (Figs. 4, 6, 8), the singular, sickle-shaped terminal apophysis (Figs. 5, 7, 9), and the embolus tip hidden

behind the median apophysis (Fig. 10). Females (Figs. 11-16) can be separated by the existence of an undulation along the posterior-lateral edge of the atrium (Fig. 11, arrow), the corresponding median septum that expands to fill the posterior portion of the atrium (Fig. 14, arrows), and the shape of the spermathecae (Figs. 16-21).

Description.—*Male (syntype)*: Total length 10.99 mm, carapace length 5.37 mm, carapace width 4.17 mm. Carapace brown with a median band of lighter hairs extending from the thoracic furrow to the PME. Other lighter hair bands radiating from the thoracic furrow. Ocular area darker between eyes. AER 0.97 mm wide, narrower than PME. PER wider posteriorly, PME 0.99 mm apart measured from center to center, PLE 1.53 mm apart from eye centers. Posterior eyes 0.49 mm in diameter, anterior eyes 0.20 mm in diameter.

Chelicerae, sternum, and coxae dark brown. Three retromarginal and three promarginal teeth. Labium dark except for light tip. Legs

Table 1.—Leg measurements in mm for *Hogna coloradensis* male syntype.

	I	II	III	IV
Femur	5.17	4.68	4.24	5.80
Patella	1.85	1.95	1.91	1.92
Tibia	4.80	4.19	3.42	3.63

brown, heavily spined. Ventral spination of leg I: femur with 1 prolateral spine, patella with 1 retrolateral spine, tibia with 3 pairs of ventral spines and 1 distal retrolateral spine, metatarsus with 1 ventral spine. Leg length: IV, I, II, III (Table 1 presents femur, patella, and tibia measurements for syntype male). Abdomen with a dark heart mark and two lighter spots along each side of the heart mark. Four chevrons follow the heart mark posteriorly. Venter pale except for a dark epigastric region and a dark spot anterior to the spinnerets. Terminal apophysis sickle-shaped, anterior region wrinkled but without prominent ridges. Embolus originating from the anterior-most region of palp, curving along retrolateral side until middle of palp (Fig. 10). Embolus tip not visible, located horizontally behind the median apophysis. Median apophysis originates from tegulum on prolateral side, triangular, appears shaped like a shark fin when viewed anteriorly. Prolateral tip of median apophysis abruptly upturned when viewed ventrally, lighter than rest of median apophysis (Fig. 10). Tip of palpal cymbium with 2 stout spines.

Female (syntypes, n = 2) (Fig. 11): Total length 13.67, 14.46 mm; carapace length 5.84, 6.53 mm; carapace width 3.94, 4.62 mm; femur I length 3.61, 5.01 mm. Coloration same as in the male except for: carapace not as covered with hair-like setae, legs with more hair-like setae, white marks on abdomen more visible. Epigynum is red, the anterior margin is heavily sclerotized with double anterior hoods. Median septum approximately one-half width of atrium anteriorly, expanding into lateral cavities just posterior to the middle of the atrial cavity (Fig. 11). Posterior end of median septum inverted T-shaped, as wide as or slightly wider than atrial cavity at its widest, not excavated on ends.

Variation.—*Hogna coloradensis* has many size, genitalic, and color variations evident throughout its range (Figs. 1, 12–21). Overall

male total length can range from 9.49–13.76 mm (*n* = 8) and female total length can range from 10.50–20.10 (*n* = 6). The male syntype has a row of three spines on the distal end of the pedipalpal femur; however, every other *H. coloradensis* examined, including the female syntypes, have four spines.

Spiders collected in Colorado match Banks' syntypes in all respects; however as specimens progress south, variations become more evident. Southern Arizona, western New Mexico and south into northern Mexico may see the atrial undulations of the epigynum diminish until they are almost not visible when viewed ventrally (Figs. 12–15); however, upon being cleared they are evident. The atrium may also take on a more rectangular shape (Fig. 15). There is variation throughout the species' range in the shape of the narrow arm of the spermatheca as well (Figs. 16–21).

One set of spiders collected from Monahans Sandhills State Park in Texas showed more variation than normal. These spiders are smaller and lacked almost all of the characteristic dark coloration on the venter of the abdomen (Fig. 2). The epigynum differed in that the atrium was shorter and the posterior T section of the median septum was thicker than usual (similar to Fig. 14). Also the spermathecae appear thinner (Fig. 17). The male palp appears consistent with other specimens including the syntype except that, in some of the specimens, the upturned end of the median apophysis has a notch where, in other specimens, a continuous thin membrane exists (Fig. 6, arrow). Light colored males were also found from the Jornada Range in Dona Ana County, New Mexico.

Another area of variation appears in southeast New Mexico. These spiders have the ventral area between the epigastric furrow and the spinnerets filled in with dark spots. The spots are organized into two or three longitudinal rows (Fig. 3). The palpal characteristics and the epigynal characteristics match the general description of *H. coloradensis*. Because there is much variation in *H. coloradensis* regarding the thickness of the spots found on the venter of the abdomen these specimens are assumed to be a dark variation of *H. coloradensis*.

Specimen notes.—The syntypes of *L. coloradensis* were apparently dried out and relaxed in 1958. Banks (1894) reported 2 males and 2 females collected, however the vial con-

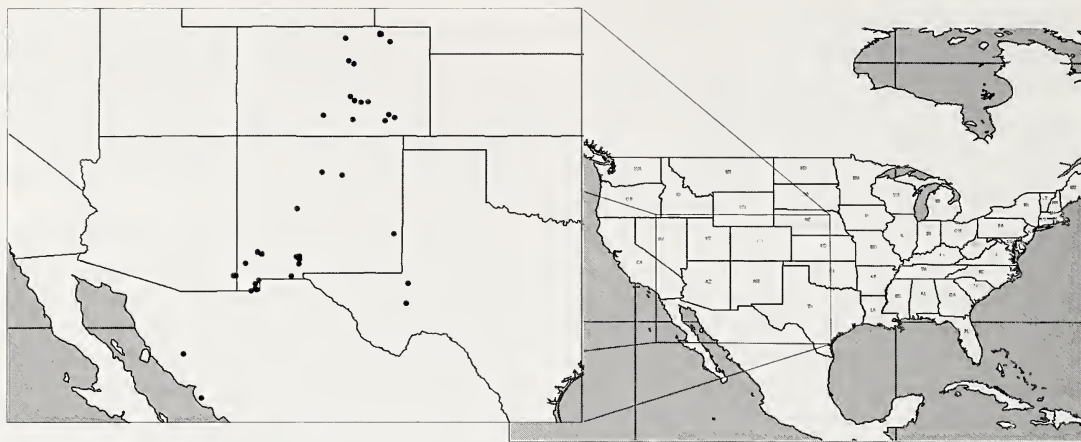


Figure 22.—Specimen localities of *Hogna coloradensis*.

tains only 1 male. The abdomen of one of the females is separated and the spider shows damage from being dried out.

In Muma's 1980 paper his *Lycosa* sp. nr. *coloradensis* is the darker variation noted above. Several other vials from AMNH and DPI identified by either Gertsch or Muma were also identified as *Lycosa* sp. nr. *coloradensis*. These specimens were clearly not *H. coloradensis* but were, instead, *Geolycosa rio-grande* (Wallace 1942), *G. missouriensis* (Banks 1895), *Hogna baltimoriana* (Keyserling 1877), or were the dark variation of *H. coloradensis*.

Habitat and behavior.—In a study of a sandy dune environment vs. a rangeland environment in New Mexico, *H. coloradensis* (*Lycosa coloradensis* in text) was one of the dominant species in the sandy environment and almost absent from the rangeland environment (Muma 1980). The sandy dune area consisted of barchan and parabolic dunes with sparse shrubby vegetation in the interdunal area. Half of the traps were set on the advancing side of a barchan dune (Muma 1980). Another study comparing a Piñon-Juniper forest to a grassland ecosystem, also in New Mexico, found that *H. coloradensis* was almost absent from the Piñon-Juniper study area (Muma 1974, 1980). The grassland was a sand-clay alluvium with some gravelly rocks dominated by low grasses and shrubs and was actively used as rangeland. This spider was also found in a mixed rangeland/grassland by Gertsch & Reichert (1976) and was also collected in a similar habitat from southeastern

Colorado using a headlamp at night (JS pers. obs.).

Spiders from Monahans Sandhills State Park in Texas were described as being obligate burrowers and showing distress when access to the burrow was blocked (Jack Brookhart pers. obs.). Muma (1975) mentions *H. coloradensis* as a burrower; however, in the lab some spiders will construct their own burrows while other *H. coloradensis* will readily use vials inserted into the substrate as burrows (JS pers. obs.). The spider has been collected from small mammal and other burrows. The burrow made by *H. coloradensis* is a small, shallow (about 5–15 cm deep), straight burrow, however the burrow may angle if an obstacle is encountered. These burrows lack the turret found in *Geolycosa* burrows. Instead, they appear to line the entrance of the burrow with silk. The spider also uses small rocks and debris to close the burrow entrance. The spider appears to use the burrow as a retreat during the day, roaming at night for prey. This behavior is similar to that of *H. carolinensis* (Walckenaer 1805) (JS pers. obs.). They have also been seen digging after prey (JS pers. obs.).

Distribution.—*Hogna coloradensis* has been found from northern Mexico northward through eastern Arizona, New Mexico, and Colorado to the Wyoming border (Fig. 22). It also is found in western Texas. Chamberlin (1908) makes note of it being found in Kansas and Nebraska; however, those specimens could not be located for verification. The spider is also mentioned in Rapp (1980) as being

found in Mitchell, Nebraska; however, those specimens also could not be found to verify and the record may be from a direct quote out of Worley (1927). Nevertheless, the western edge of both those states as well as southern Wyoming would have suitable habitats. This species does not appear to extend into the great basin area of Utah.

This project was supported by National Science Foundation grant DBI-0346378 awarded to PEC. Thanks to Charles Dondale for useful discussions relating to this study. Thanks also to Mark Harvey and Volker Framenau for helpful comments and suggestions.

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Manuscript received 15 December 2005, revised 6 April 2006.

SOSIPPUS REVISITED: REVIEW OF A WEB-BUILDING WOLF SPIDER GENUS FROM THE AMERICAS (ARANEAE, LYCOSIDAE)

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ABSTRACT. The systematic status of the wolf spider genus *Sosippus* Simon 1888 is reviewed. Males of four species: *S. placidus* Brady 1972, *S. janus* Brady 1972, *S. michoacanus* Brady 1962 and *S. agalenooides* Banks 1909 are described and fully illustrated for the first time. A cladistic analysis based upon twelve morphological characters resulted in two distinct species-groups within *Sosippus*. One species-group of the genus occurs from Georgia and Florida in the southeastern United States, westward along the Gulf Coast to south Texas. A second species-group occurs in Arizona and California, and is found in Mexico and Central America as far south as Costa Rica. A new key to the ten species of *Sosippus* now recognized is presented and updated to include male characters and other features. Collections and observations since earlier studies have provided new information about the social behavior and more widespread distribution of *Sosippus janus*. Maps have been reconstructed to update the ranges of all species. A preliminary cladistic analysis of the nine species of *Sosippus* for which both genders are known is presented. Additional critical drawings are provided to illustrate features in the character analysis and facilitate use of the key.

Keywords: Systematics, phylogeny, new descriptions, Nearctic, Neotropical.

Previous studies (Brady 1962, 1972) revealed *Sosippus* Simon 1888 to be unique among lycosids in several traits. The genus was originally placed in the subfamily Hippasinae because of its elongated spinnerets associated with its web building behavior. In comparing *Sosippus* to species of *Hippasa* Simon 1885, little similarity was found in any diagnostic features, and the existence of any close relationship between *Sosippus* and the other Hippasinae is doubtful. Dondale (1986) in his studies of the subfamilies of Lycosidae placed *Sosippus* [together with *Porrimosa* Roewer 1960 (now *Aglaoctenus* Tullgren 1905) and its relatives] in the new subfamily Sosippinae. Dondale's decision was based upon characteristics of the male palpus: (1) the loss of the terminal apophysis, (2) the tegular groove functioning as a conductor, and (3) the embolus lying among a cluster of tegular processes. According to Dondale the sister group of the Sosippinae is represented by all subfamilies of lycosids taken together. A recent analysis of combined 12S rRNA, 28S rRNA and NADH1 mtDNA genes by Murphy et al. (2006) recognized a distinct clade that includes *Sosippus placidus* Brady 1972 and

Aglaoctenus lagotis (Holmberg 1876), supporting their recognition as members of a separate subfamily.

A particular feature of zoogeographical interest is the restricted distribution of *S. placidus* in south central Florida in an area defined as Red Hill Island. During the Aftonian Interglacial period Red Hill was the southernmost island in a series of islands that occurred where the Florida peninsula now stands (Laesle 1958). Brady (1972) suggested two factors influencing this insular pattern. First, open water gaps between the Pleistocene islands that could have served as effective barriers to species dispersal between the islands, and secondly, and more convincingly, the reduction in population numbers on these Pleistocene islands producing a corresponding reduction in genetic variability that could have facilitated speciation. In terms used by Ernst Mayr (1963), a genetic revolution would have occurred. In synopsis, the geographical isolates would have become genetically homogeneous and ecologically specialized for the conditions on the Pleistocene islands. As these islands were joined after the Pleistocene, the insular populations remained effectively isolated eco-

logically and reproductively. The present day distribution pattern of two species, *S. placidus* and *S. janus* Brady 1972 (to a lesser extent), fit well with the configuration of islands during the Pleistocene; however, the saltwater barriers between islands may not have been so great as to overcome the ability of most spiders to balloon.

The emerging factor that was missing from this original hypothesis (Brady 1972) is the observation of sub-social behavior in several species of *Sosippus* and the concomitant lack of long-range dispersal. Many lycosid spiderlings are known to balloon soon after leaving the dorsum of the abdomen of the female where they are first lodged after hatching from the egg case. The female is instrumental in dispersal as she moves about. But unlike many other lycosid species, the young of *Sosippus* remain with the female for long periods. Upon hatching from the egg sac and riding on the female's abdomen for some time the young remain in the web with the female (Brach 1976). Since the females do not leave the funnel web, the young do not scatter, and ballooning has not been observed. Thus, dispersal is strictly limited, reinforcing the endemism characteristic of the above two species. Once populations of *Sosippus* are separated, they will tend to disperse very slowly even in the absence of significant geographic barriers. In 1997 observations of *S. janus* in my own laboratory confirmed that the young remain with the female in the web even after several molts. When both species were contained in five-gallon terraria, the young of *S. janus* were observed to be much more tolerant of one another than the young of *Allocosa georgicola* (Walckenaer 1837) under similar conditions. In several instances the young of *S. janus* participated in group feeding after the female had captured large prey items (crickets). The young alone were not able to utilize large prey items. The study of *Sosippus*, involving its phylogenetic relationships to other Lycosidae, its ecological and geographical distribution pattern, and its sub-social behavior, continues to raise many interesting questions.

METHODS

The procedures for illustrations and color descriptions as well as methods for measure-

ments are described in Brady (1962, 1979). All measurements are in millimeters.

Specimens are lodged in the following institutions: American Museum of Natural History, New York (AMNH); Museum of Natural History, London (BMNH); California Academy of Sciences, San Francisco (CAS); Florida State Collection of Arthropods, Gainesville (FSCA); Hope College Collection, Holland, Michigan (HCC); Museum of Comparative Zoology at Harvard, Cambridge, Massachusetts (MCZ); and Museum National d'Histoire Naturelle, Paris (MNHN).

Phylogenetic analysis.—Species belonging to *Sosippus* were selected as the in-group members: *S. placidus*, *S. floridanus* Simon 1898, *S. janus*, *S. minus* Chamberlin 1924, *S. texanus* Brady 1962, *S. californicus* Simon 1898, *S. michocanus* Brady 1962, *S. mexicanus* Simon 1888, and *S. agalenoides* Banks 1909. Since *S. plutonus* Brady 1962 is still known only from a single female and the male has not been discovered, it has been excluded from the study. The genus *Aglaoctenus* serves as the out-group in the cladistic analysis with the type species *Aglaoctenus lagotis* (C.L. Koch 1847) serving as the exemplar. Species in *Aglaoctenus* and *Sosippus* make up the primary members of the subfamily Sosippinae as defined by Dondale (1986). The recognition of this subfamily was based upon characteristics of the male palpus: (1) the loss of the terminal apophysis, (2) the tegular groove functioning as a conductor, and (3) the embolus lying among a cluster of tegular processes. Because they are encountered much more frequently in the taxonomic literature, attention is called here to the generic names *Porrinula* Roewer 1960 and *Porrinosa* Roewer 1960, previously used for the species now described under *Aglaoctenus* (Capocasale 1982, 1991). *Aglaoctenus* Tullgren 1905, is a senior synonym of *Porrinosa* Roewer, contra to the decision by Carico (1993). The status of *Aglaoctenus* was clarified by Santos & Brescovit (2001) in a revision of that South American spider genus. The reasons for these changes in generic placement are summarized in Platnick (2006).

Sosippus and *Aglaoctenus* are the only New World genera of Lycosidae reported to build sheet webs with funnel-shaped retreats. Concomitant to this activity is the presence of elongate posterior spinnerets. Another notable feature in species of these two genera is the

Table 1.—Morphological data matrix used for the cladistic analysis of *Sosippus* species. Character numbers are the same as those described in the text.

Species	Characters											
	0	1	2	3	4	5	6	7	8	9	10	11
<i>Sosippus texanus</i>	0	0	0	0	0	1	1	0	1	1	1	1
<i>Sosippus placidus</i>	0	0	0	0	0	1	1	1	1	1	1	1
<i>Sosippus minus</i>	0	0	0	0	0	1	1	0	1	1	1	1
<i>Sosippus michoacanus</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Sosippus mexicanus</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Sosippus janus</i>	0	0	0	0	1	1	1	0	1	1	1	1
<i>Sosippus floridanus</i>	0	0	0	0	1	0	1	0	1	1	1	1
<i>Sosippus californicus</i>	0	0	0	0	0	0	0	0	0	0	1	0
<i>Sosippus agelenoides</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Aglaoctenus lagotis</i>	1	1	1	1	0	0	0	0	1	0	0	1

absence in the male of pedipalpal stridulatory organs, reported by Fernandez-Montraveta and Simo (2002) for *Aglaoctenus lagotis* and also true for the nine species of *Sosippus* that I have examined. In addition, the species studied have close similarities in color pattern, body structure, and male and female genital morphology. Murphy et al. (2006) also found *Sosippus* and *Aglaoctenus* to be sister-taxa. Because of the absence of comparable features in other North American Lycosidae, I found that using different lycosid species, such as *Rabidosa rabida* (Walckenaer 1837) or *Gladicosa gulosa* (Walckenaer 1837), as a second out-group, did not yield any significant insight to evolutionary relationships.

Characters and character states.—Character scoring is presented in Table 1. The character matrix consists of 12 characters. These characters are based upon somatic morphology (5), color patterns (3) and structural components of the male and female copulatory organs (4). Characters were scored through careful measurement, examination and illustration of key taxonomic components as well as observation of most species in the field.

Character descriptions.—*Somatic characters* (Fig. 1): Character 0: Anterior eye row (AER); 0 = slightly recurved (Fig. 2), 1 = strongly recurved (Fig. 3).

Character 1: Anterior lateral eye (ALE) naclles; 0 = not strongly developed (Fig. 2), 1 = well developed and directed down and outward (Fig. 3).

Character 2: Size ratio of posterior lateral eye row (PLR) width to posterior ocular quadrangle length (POQL); 0 = PLR width less

than 1.5 times POQL, 1 = PLR width greater than 1.5 times POQL.

Character 3: Size ratio of clypeus height (CLPH) to diameter of anterior median eye (AME); 0 = CLPH subequal to AME diameter, 1 = CLPH less than AME diameter.

Character 4: Number of teeth on each side of retromarginal edge of cheliceral fang groove; 0 = three teeth, 1 = four teeth.

Character 5: Color pattern on carapace; 0 = with distinct white marginal or submarginal longitudinal white stripes (Figs. 4, 7, 9–11, 12, 15); 1 = pattern diffuse, without distinct marginal or submarginal white stripes (Figs. 5, 6, 12, 13).

Character 6: Predominant coloration of carapace, produced by pigmentation of integument together with clothing of short setae or pubescence (basically the color of the spider in life or when dried); 0 = yellow to brown in appearance, 1 = gray to black in appearance.

Character 7: Color of venter of abdomen; 0 = tan to pale yellow or cream, 1 = orange or red-orange.

Female reproductive structures: Character 8: Copulatory openings (CO); 0 = oval or tear drop in shape (Figs. 31, 35, 39), 1 = narrow groove, almost linear in shape (Figs. 19, 23, 26, 27).

Character 9: Size ratio of width of anterior neck (N) of middle field (MF) to width of posterior edge of transverse piece (TP); 0 = wide, N width more than 1/3 of TP (Figs. 31, 35, 39), 1 = narrow, N width 1/3 or less than TP (Figs. 19, 23, 26, 27).

Male reproductive structures: Character 10:

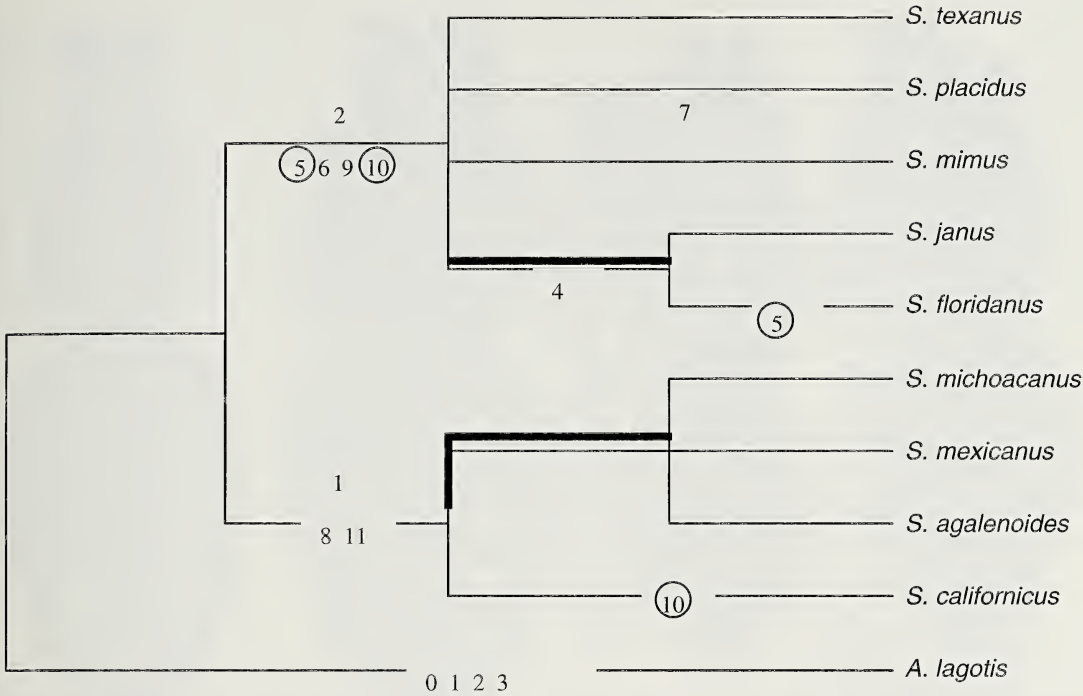
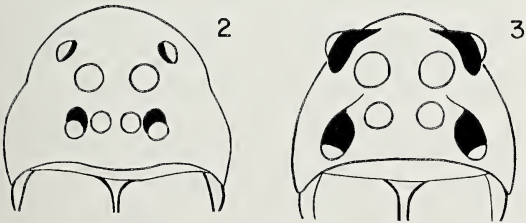


Figure 1.—A single representative of eight most parsimonious trees produced by analysis of morphological data of *Sosippus* and *Aglaoctenus lagotis* (14 steps, CI = 0.86, RI = 0.91) with character state distributions shown. Numbers above branches indicate decay values. Numbers below branches refer to characters that change along those branches (circled numbers indicate characters that are homoplasious). Bold branches collapse in the strict consensus.

Presence of finger or thumb-like conductor (C) (tegular apophysis *a* of Sierwald 2000); 0 = conductor elongate, broad and thumb-like (Figs. 28, 32, 36), 1 = conductor elongate, thin and finger-like (Figs. 16, 20, 24).

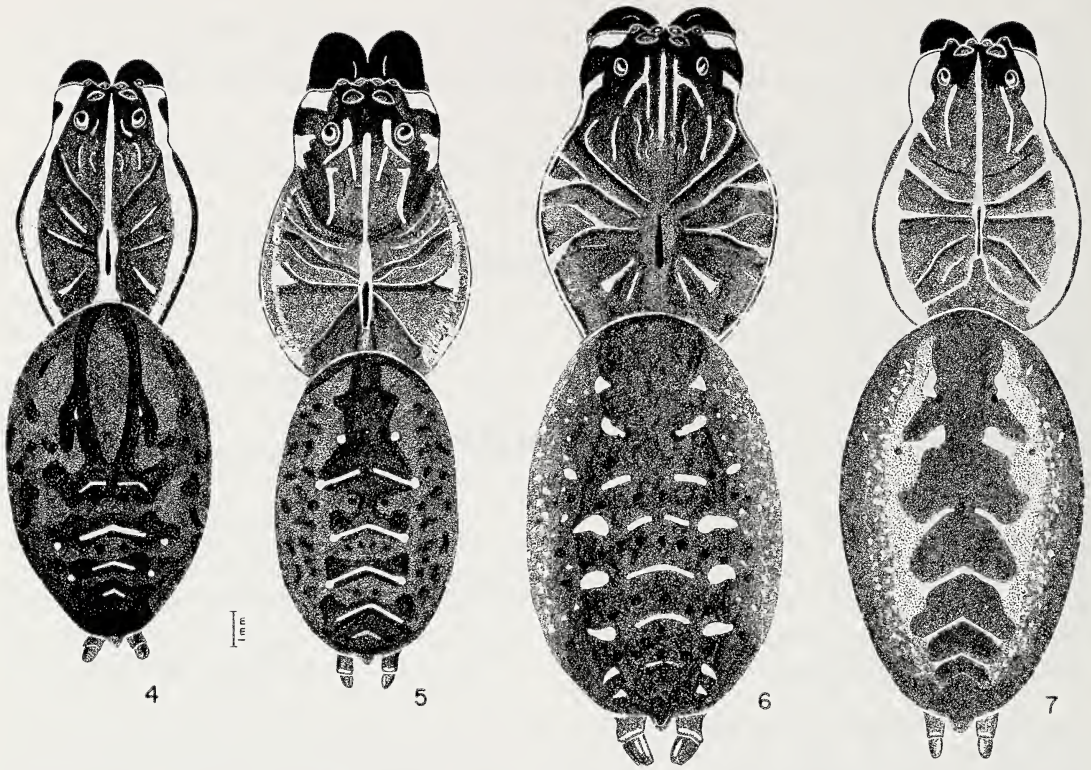
Character 11: Presence or absence of pearlescent retrolateral lobe (RL) of cymbium (CY); 0 = pearlescent lobe present (Figs. 28, 32, 36), 1 = pearlescent lobe absent (Figs. 16, 20, 24).



Figures 2, 3.—Carapace, frontal view, showing eye arrangement: 2. *Sosippus texanus*, female from Goose Island State Park, Aransas County, Texas; 3. *Aglaoctenus lagotis* (O. Pickard-Cambridge), female from Rockstone, British Guiana.

Analysis.—Nine species of *Sosippus* and one outgroup, *Aglaoctenus lagotis*, were scored for 12 morphological characters, and cladistic analyses were conducted using PAUP* version 4.0b10 (Swofford 1999). An exhaustive search was conducted, with all characters treated as unordered and assigned equal weight. Decay values were determined using AutoDecay version 5.0 (Eriksson 2001) and executed in PAUP* using the branch and bound search algorithm. When characters were optimized onto the resulting phylogeny, the DELTRAN option was selected.

Results.—Phylogenetic analyses resulted in eight most parsimonious trees (Fig. 1; 14 steps, CI = 0.86, RI = 0.91). Mapping character state distributions onto a consensus tree is not appropriate, so one tree was selected. In order to accommodate this: 1) I selected an example from the eight trees that represents zoogeographic trends seen in the group; and 2) I indicated which of the branches in the representative tree collapse in the strict consensus. Two well-supported clades were



Figures 4–7.—Dorsal view of *Sosippus* females: 4. *S. floridanus* from Highlands Hammock State Park, Highlands County, Florida; 5. *S. mimus* holotype, from Mandeville, Saint Tammany Parish, Louisiana; 6. *S. texanus* from Goose Island State Park, Aransas County, Texas; 7. *S. californicus* from Brown's Canyon, Baboquivari Mountains, Pima County, Arizona.

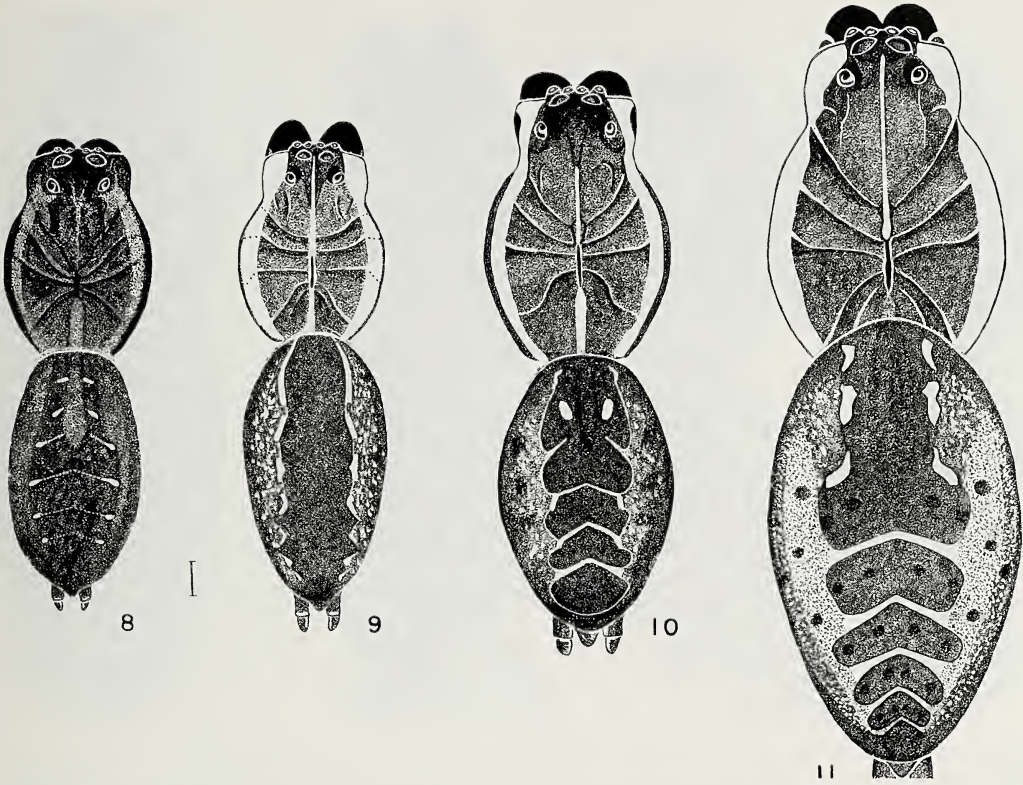
found, one containing species with a predominant eastern distribution pattern (*S. placidus*, *S. floridanus*, *S. janus*, *S. mimus*, and *S. texanus*) and the other clade with species in the western United States, Mexico, and Central America (*S. californicus*, *S. michoacanus*, *S. mexicanus*, *S. agalenoides*). No resolution was found within either clade.

Discussion.—The subfamily Sosippinae, represented predominantly by *Sosippus* and *Aglaotenus*, is defined by its web-building behavior and elongate posterior spinnerets. Dondale (1986) cites the loss of the terminal apophysis, the tegular groove functioning as conductor, and the embolus lying among a cluster of tegular apophyses as diagnostic characters of this subfamily. The absence of male stridulatory organs at the tibio-palpal joint and the lack of macrosetae at the distal end of the palpus are shared characters of this clade (Fernandez-Montraveta & Simo 2002). The recognition of the subfamily Sosippinae is also supported by a worldwide investigation

of Lycosidae undertaken by Murphy et al. (2006) using molecular markers. Color patterns on the carapace, as illustrated in this paper, and the morphology of the male and female genital organs also separate sosippines from other lycosids.

Aglaotenus lagotis is distinguished from *Sosippus* primarily by the arrangement and development of the eye rows (Table 1). Characters 0, 1, 2 and 3 clearly separate *Aglaotenus lagotis* from *Sosippus* and emphasize the dramatic differences in eye arrangement between these two genera. Although showing similarities, the male and female genital morphology are also quite distinct. These similarities and differences can be seen by comparing illustrations of the two genera.

Number of retromarginal cheliceral teeth (Character 4), pigmentation of the carapace (Character 6) and venter (Character 7) are rather general (pleisiomorphic) characters shared by *Sosippus* and *Aglaotenus*. They occur in other lycosids. The color pattern on the cara-

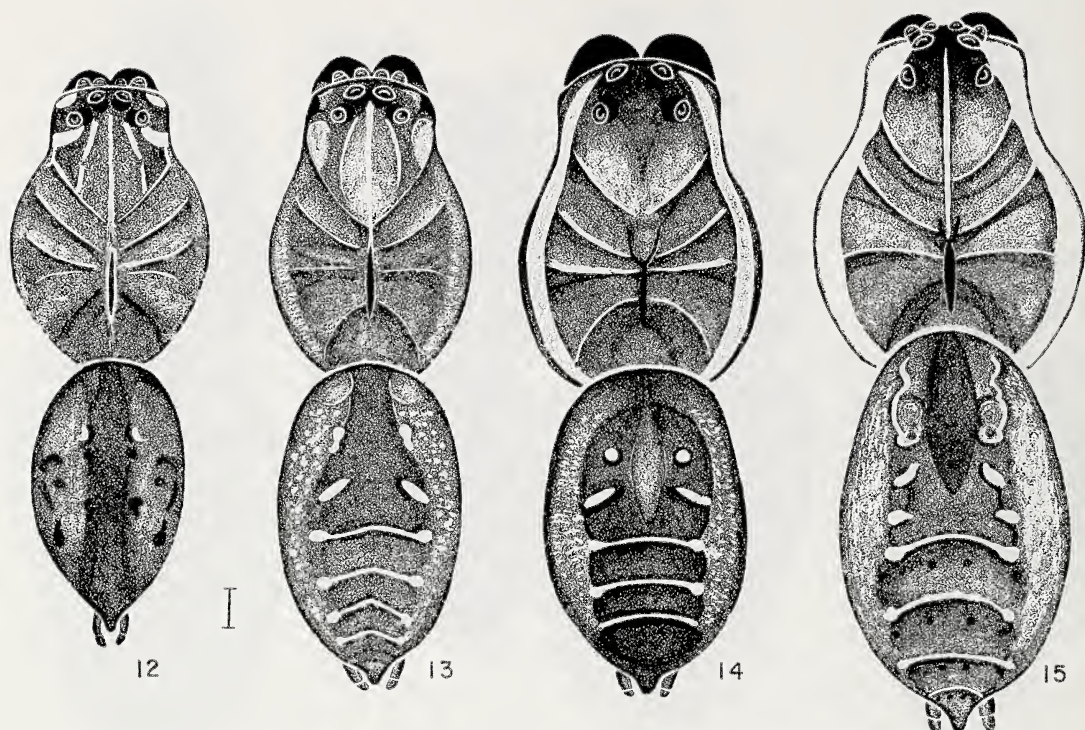


Figures 8–11.—Dorsal view of *Sosippus* females: 8. *S. plutonus* holotype, from Tenango del Valle, Mexico, Mexico; 9. *S. mexicanus* from Acapulco de Juarez, Guerrero, Mexico; 10. *S. michoacanus* holotype, from Tzaracua Falls, 11 km. from Uruapan, Michoacan, Mexico; 11. *S. agalenoides* syntype, from Puntarenas, Puntarenas, Costa Rica.

pace (Character 5) and morphology of the reproductive structures (Characters 8, 9, 10, 11) represent more specific characters (synapomorphies) separating them from other clades, but shared within the subfamily Sosippinae. However, these characters are clearly distinct between *Aglaoctenus* and *Sosippus*, and support their recognition as separate genera.

Examination of *Sosippus* from a geographic perspective, as well as morphological examination, allows for some interesting phylogenetic speculation. In general *Sosippus* appears to have originated in a tropical or subtropical climate (Central America) and then expanded northward into North America, diverging into eastern and western clades. In the eastern clade the same number of 3-3 retromarginal teeth (Character 4) and diffuse color pattern (Character 5) can be traced, beginning with *S. texanus* in southern Texas, to *S. minus* from Louisiana to western Florida, and south to the Lake Placid population of *S. placidus*. The

pattern of 4-4 retromarginal teeth in *S. janus* and *S. floridanus* appears to be a derived character and links these two species. However, *janus* retains the diffuse color pattern linking it with *S. minus* and *S. placidus*, suggesting that *S. floridanus* may be the most recently derived species. In the western clade, which is connected with the Mexican and Central American species, a phylogenetic pattern is more difficult to discern. *Sosippus californicus*, *S. michoacanus*, *S. mexicanus* and *S. agalenoides* share yellow-brown pigmentation (Character 6), the presence of a pearlescent retrolateral lobe on the cymbium (Character 11), and a relatively wide anterior neck on the middle field of the epigynum (Character 8). Geographically it appears that *S. californicus* is a recently derived species and that *S. agalenoides* with its more southerly distribution may link *Sosippus* to *Aglaoctenus*. However, *S. michoacanus* appears closer to *Aglaoctenus lagotis* in structure of the male palpal organ



Figures 12–15.—Dorsal view of *Sosippus* males. 12. *S. janus* from Welaka Reserve, Welaka, Putnam County, Florida; 13. *S. placidus* from 9.6 km S. of Lake Placid, Highlands County, Florida; 14. *S. mi-choacanus* from 12.8 km SW of Colima, Colima, Mexico; 15. *S. agalenoides* from Puntarenas, Puntarenas, Costa Rica.

and the female epigynum, which might qualify it for the closest link to an ancestral clade connecting *Sosippus* and *Aglaoctenus*.

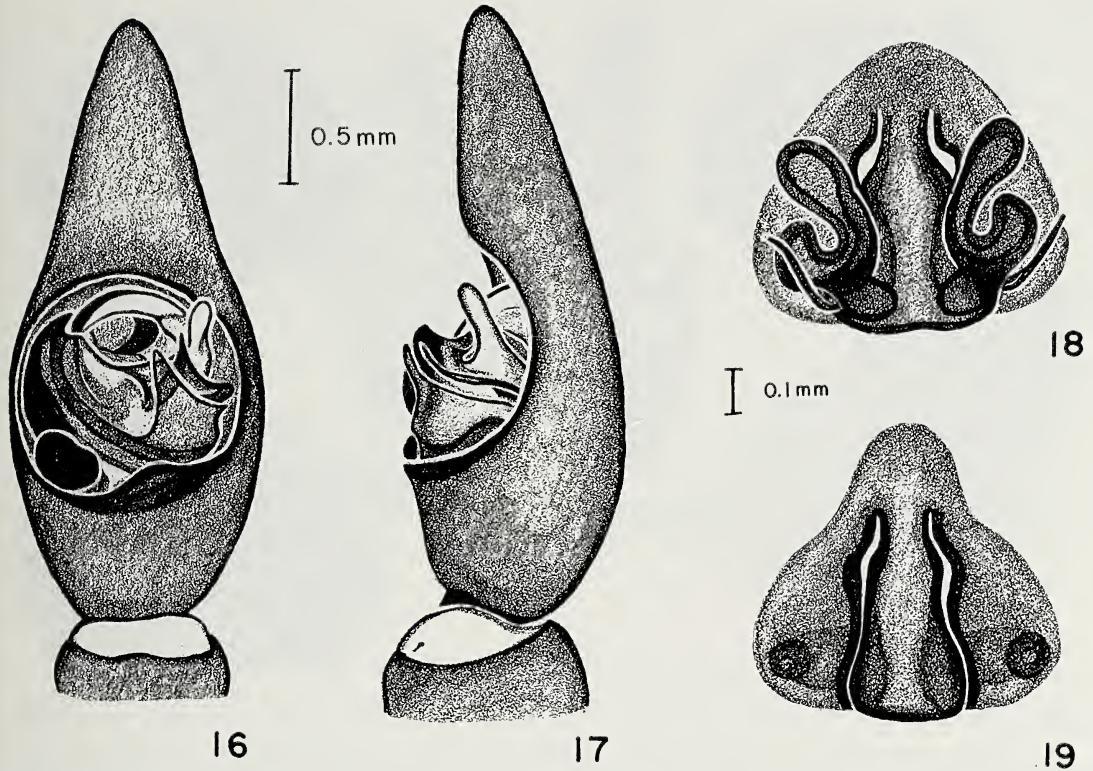
Mexican species of *Sosippus* have not been well-collected and it is possible that other species are present in Mexico and Central America. The varied topography, different biomes and varied vegetation of this region provide physical conditions for speciation. Because of its specialized habits that limit dispersal, it is very likely that additional species of *Sosippus* exist there. Much more work needs to be done in the field and laboratory to elucidate the phylogenetic relationships of species described in *Sosippus* and *Aglaoctenus*.

Methods.—An explanation of the methods used in making measurements, as well as for color descriptions and illustrations is provided in Brady (1962). The measurement of the posterior ocular quadrangle (POQ) is illustrated in fig. 1. However, the line tangent to the anterior most part of the PME, rather than the line tangent to the AME, is now used in mea-

suring the length of the carapace and total body length.

In the Key to Species "Figs." (capitalized) refer to figures included in this paper, while "figs." (not capitalized) refer to figures in previous papers. The figures in this paper, other than those of newly described males, were carefully chosen to facilitate use of the key and elucidate characters used in the cladogram. The Key to Species can be readily used without reference to figures from previous papers. The earlier references (figs.) are for systematists who might want to see variation in genitalic structure, or follow the changes in nomenclature of *Sosippus* populations in Florida.

Under Material Examined for species that are relatively rare or uncommon, I have cited all of the records (both old and new). For species that are common, with many records from earlier publications, I have added new records only, and so indicated. Where new records are not indicated, it means that all of the records of examined specimens are listed.



Figures 16–19.—*Sosippus placidus*. 16, 17. Male from 9.6 km S. of Lake Placid, Highlands County, Florida: 16. Left palp, ventral view; 17. Left palp, retrolateral view. 18, 19. Female from 9.6 km S. of Lake Placid, Highlands County, Florida: 18. Vulva, dorsal view; 19. Epigynum, ventral view.

TAXONOMY

Family Lycosidae Sundevall 1833

Sosippus Simon 1888

Sosippus Simon 1888:206.

Sosippinus Roewer 1955:923. First synonymized by Brady 1962:131.

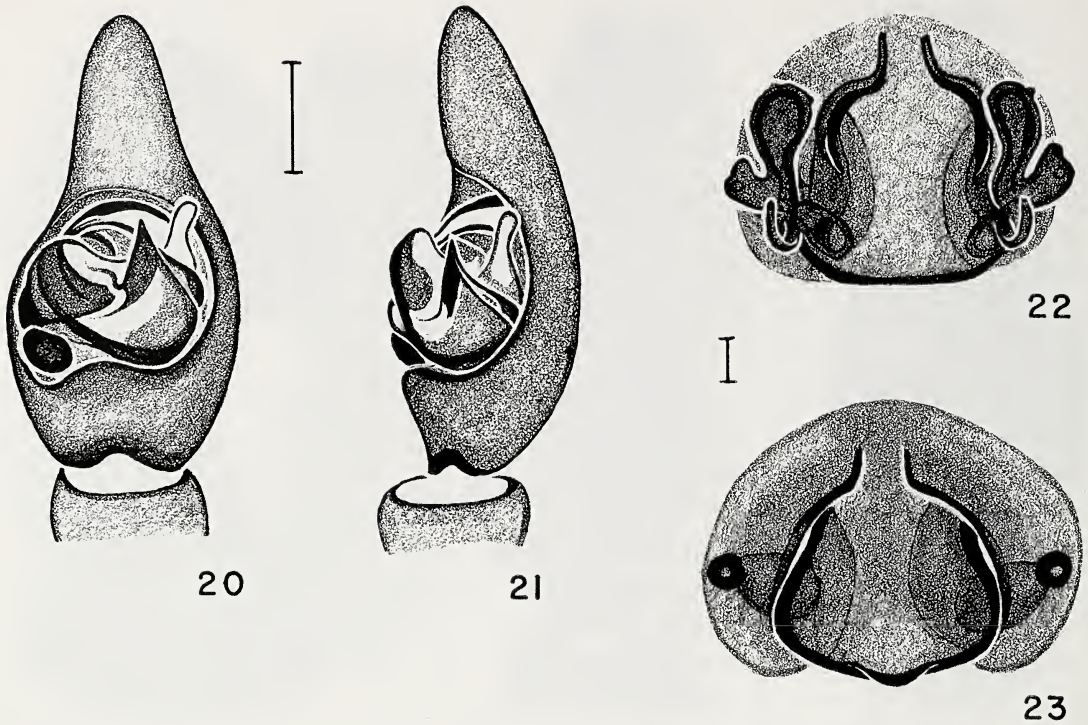
Hippasella Mello-Leitao 1944:342. First synonymized by Capocasale, 1990:140.

Type species.—*Sosippus*: *Sosippus mexicanus* Simon 1888. The problem of the type species has been discussed by Bonnet (1958). Simon (1888) established the genus *Sosippus* and designated *Dolomedes oblongus* C.L. Koch 1847 [now *Aglaoctenus oblongus* (C.L. Koch)] as the type. At the same time he described *Sosippus mexicanus* as a new species. In 1898 Simon transferred *D. oblongus* to the genus *Diapontia* Keyserling 1876 and designated *S. mexicanus* as the type species of *Sosippus*. *Sosippus mexicanus* has been assumed to be the type for the past 108 years. For the sake of nomenclatural stability, I followed the decision reached by Bonnet.

Sosippinus: *Sosippus californicus* Simon, 1898a, by original designation.

Hippasella: *Hippasella nitida* Mello-Leitao, 1944, by original designation.

Diagnosis.—Anterior eye row (AER), as seen from in front, procurved (Fig. 2) Anterior lateral eyes (ALE) subequal to anterior median eyes (AME) and mounted on distinct tubercles. AER wider than posterior median eye row (PMR), the PLE row wider than the anterior row. Chelicerae robust, with prominent bosses. Anterior cheliceral margin with three teeth on each side, the central tooth largest. Posterior cheliceral margin with three or four teeth on each side (rarely five); usually constant within a species. Labium longer than wide, as long as wide, or slightly wider than long. Endites heavily scopulate, slightly converging in front of labium, which is less heavily scopulate. Carapace with conspicuous longitudinal thoracic groove or foveae. Carapace of females highest in the cephalic region, of males usually highest in the thoracic region. Sternum always longer



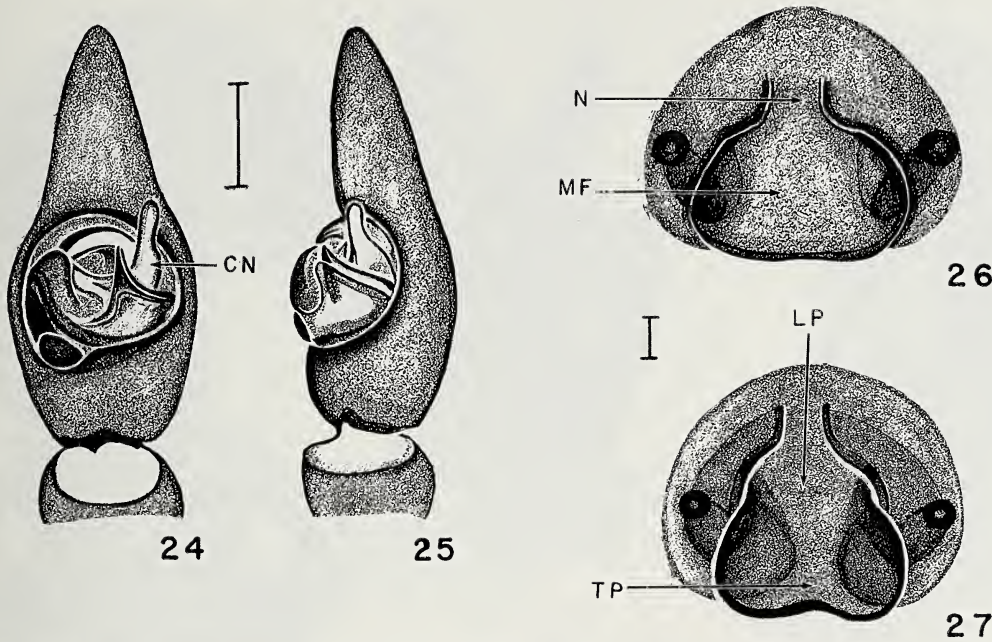
Figures 20–23.—*Sosippus janus*. 20, 21. Male from NE. shore of Lake Lochloosa, Alachua County, Florida: 20. Left palp, ventral view; 21. Left palp, retrolateral view. 22, 23. Female from NE shore of Lake Lochloosa, Alachua County, Florida 22. Vulva, dorsal view; 23 Epigynum, ventral view.

than wide. Order of leg length: IV, I, II, III. Leg IV longest. Tarsi and metatarsi of legs I and II heavily scopulate; tibia I and II usually scopulate at distal ends. Males with legs longer than those of females and more heavily scopulate. For a more detailed discussion of the

number of teeth on the posterior margin of the chelicerae, used as a diagnostic character at the generic level by previous authors, see Brady (1962, 1972). Sierwald (2000) was mistaken about *S. mimus* having four posterior cheliceral teeth on each side.

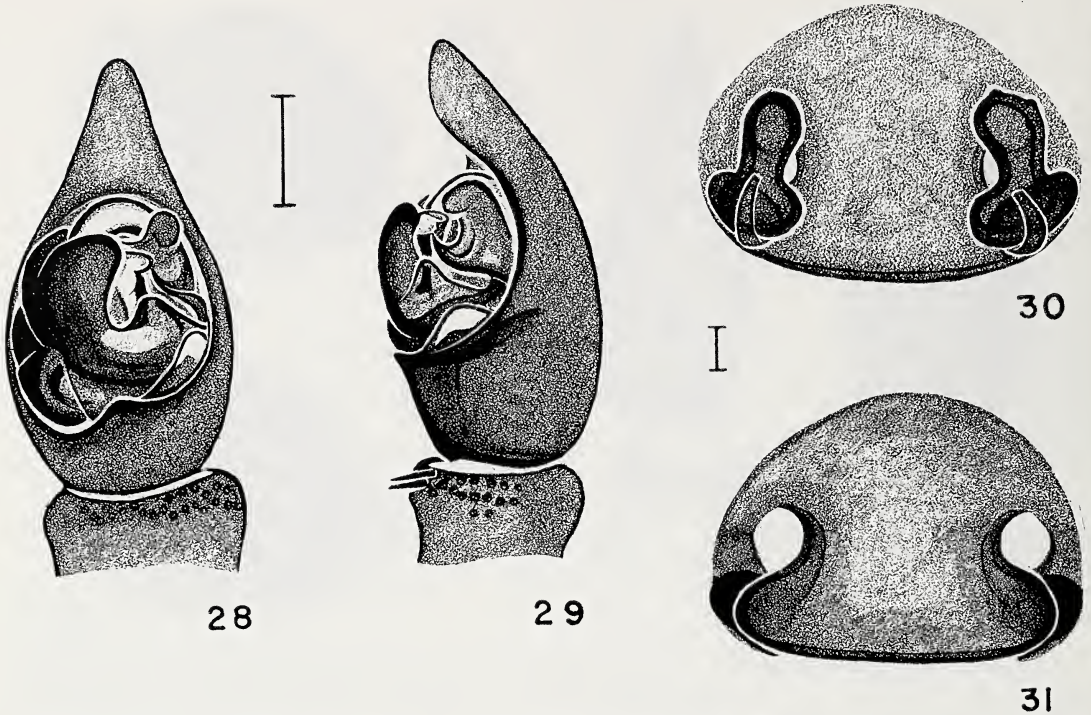
KEY TO SPECIES

- 1. Four posterior cheliceral teeth 2
- Three posterior cheliceral teeth 3
- 2(1). Carapace with a distinct white median stripe beginning at second eye row and continuing to posterior edge; and with two broad white submarginal stripes as in Fig. 4. Epigynum as in Fig. 26, figs. 18, 19 (Brady 1962), figs. 10–13, 19–24 (Brady 1972). Palpus as in figs. 40–43 (Brady 1962). Throughout Florida Peninsula *Sosippus floridanus*
- Carapace without a distinct median white stripe running length of carapace, and without distinct white submarginal stripes as in Fig. 12. Epigynum as in Figs. 22, 23, 27, figs. 14–18 (Brady 1972). Palpus as in Figs. 20, 21. Northern Florida and southern Georgia *Sosippus janus*
- 3(2). Sternum and ventral surface of abdomen bright orange. Dorsal pattern as in Fig. 13. Epigynum as in Figs. 18, 19, figs. 25–27 (Brady 1972). Palpus as in Figs. 16, 17. Southern Florida near Lake Placid *Sosippus placidus*
- Sternum and ventral surface of abdomen cream to brownish yellow 4
- 4(3). Without a conspicuous median white stripe running length of carapace and without distinct submarginal white stripes 5
- With a definite median white stripe beginning behind second eye row and continuing to posterior edge of carapace, and with distinct broad white marginal or submarginal stripes 7



Figures 24–27.—*Sosippus* species. 24, 25. *S. mimus*. Male from Fountain Bleu State Park, Saint Tammany Parish, Louisiana: 24. Left palp, ventral view; 25. Left palp, retrolateral view. 26. *S. floridanus*. Female from 1.6 km E of Horse Creek, De Soto County, Florida. 27. *S. janus*. Female from Okefenokee Swamp State Park near Waycross, Ware County, Georgia. Abbreviations: CN, conductor of embolus; LP, longitudinal piece of middle field of epigynum; MF, middle field of epigynum; N, neck of MF of epigynum; TP, transverse piece of MF of epigynum.

- 5(4). Mostly black in color without distinct lighter markings as in Fig. 8. Epigynum as in figs. 25, 26 (Brady 1962). High elevations in Mexico *Sosippus plutonus*
Dark brown or gray with distinct white dashes behind posterior lateral eyes (PLE) and white dots on dorsum of abdomen as in Figs. 5, 6, figs. 3, 4 (Brady 1962) 6
- 6(5). Dorsal pattern as in Fig. 5. Epigynum as in figs. 15, 16 (Brady 1962), figs. 19–24 (Brady 1972). Palpus as in Figs. 24, 25, figs. 34, 35 (Brady 1962). North and western Florida to eastern Louisiana *Sosippus mimus*
Dorsal pattern as in Fig. 6. Epigynum as in figs. 21, 22 (Brady 1962). Palpus as in figs. 37–39 (Brady 1962). Found in southern Texas *Sosippus texanus*
- 7(4). Abdomen with wide median brown stripe bordered by white lines at the anterior end; these lines broken into a series of posterior white dashes. No white chevrons crossing the wide median brown stripe, as in Fig. 9. Epigynum as in figs. 23, 24 (Brady 1962). Palpus as in figs. 46, 47 (Brady 1962) *Sosippus mexicanus*
Abdomen with wide median brown stripe with indentations accented by white spots anteriorly and with a series of white chevrons crossing the median stripe posteriorly as in Figs. 7, 14, 15 8
- 8(7). Epigynum with a broad neck and greatly expanded median field as in Figs. 30, 31. Palpus as in Figs. 28, 29 *Sosippus michoacanus*
Epigynum with a relatively narrow neck and rounded (spade-shaped) median field as in Figs. 34, 35, 38, 39. Palpus as in Figs. 32, 33, 36, 37 9
- 9(8). Dorsal pattern as in Fig. 7. Epigynum as in figs. 27, 28 (Brady 1962). Palpus as in figs. 44, 45 (Brady 1962) *Sosippus californicus*
Dorsal pattern as in Figs. 11, 15. Epigynum as in Figs. 34, 35, 38, 39, figs. 29, 30 (Brady 1962). Palpus as in Figs. 32, 33, 36, 37 *Sosippus agalenoides*



Figures 28–31.—*Sosippus michoacanus*. 28, 29. Male from 12.8 km SW of Colima, Colima, Mexico: 28. Left palp, ventral view; 29 Left palp, retrolateral view. 30, 31. *S. michoacanus*. Female from 12.8 km SW of Colima, Colima, Mexico: 30 Vulva, dorsal view; 31 Epigynum, ventral view.

Sosippus placidus Brady 1972

Figs. 13, 16–19, 40

Sosippus mimus [in part]: Brady 1962:156, figs. 34, 35.

Sosippus placidus Brady 1972:46, figs. 25–27, 39; Platnick 1997:585; Sierwald 2000:134, figs. 1–9; Platnick 2006.

Material examined.—*Type*: USA: *Florida*: Highlands County: Holotype female, 9.6 km S. of Lake Placid, 27°11'N, 81°21'W, 12 June 1968, A.R. Brady, J. Toothaker (MCZ).

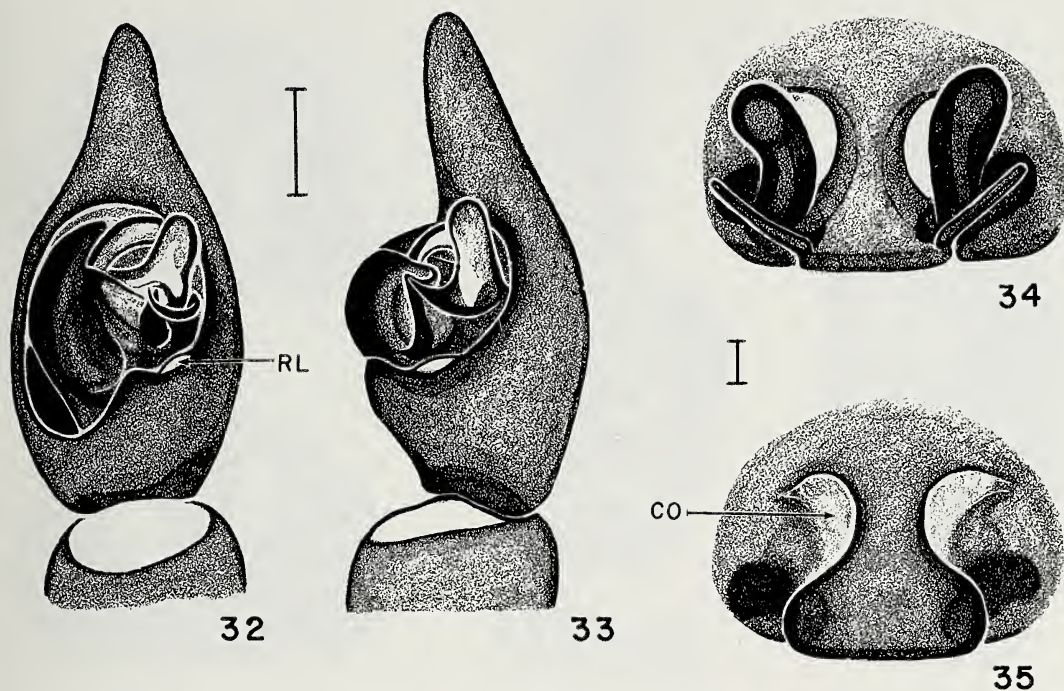
Other material: USA: *Florida*: Highlands County: 12 juveniles, Archbold Biological Station near Lake Placid, 27°11'N, 81°21'W, 24 January–4 February 1943, M. Cazier (AMNH); 2 ♀, 7 juveniles, 9.6 km S. of Lake Placid, 12 June 1968, A.R. Brady, J. Toothaker (HCC); 1 ♂, 3 ♀, same location, 1 June 1973, A.R. Brady (HCC); 2 ♂, 4 ♀, 1 juvenile, same location, 29 June 1978, A.R., M.A., K.D. Brady (HCC).

Etymology.—Latin adjective derived from geographic locality, Lake Placid, Florida.

Diagnosis.—*Sosippus placidus* is recog-

nized by its striking red-orange ventral surface, 3-3 posterior cheliceral teeth, and distinct epigynum (Figs. 18, 19). It differs from *S. floridanus*, its closest relative geographically, in number of cheliceral teeth (*floridanus* with 4-4), color pattern (compare Fig. 13 with Fig. 4), and structure of the epigynum (compare Figs. 18, 19 with Fig. 26 and figs. 18, 19 (Brady 1962), figs. 10–13, 19–24 (Brady 1972)). *Sosippus placidus* agrees somewhat with *S. mimus* in dorsal color pattern (compare Fig. 13 with Fig. 5), but is distinguished from that species by its red-orange ventral surface, distinct epigynum, and geographic location.

Color.—*Female*: Pattern as in fig. 39 (Brady 1972). Face dark reddish brown with broad marginal stripes of paler orange-brown due to covering of white setae. Pattern of dark lines radiating from thoracic groove as in male. Dorsum of abdomen dark brown with five pairs of white spots connected by white chevrons on posterior half. Venter of abdomen bright yellow-orange. Legs brown with alter-



Figures 32–35.—*Sosippus agalenoides*. 32, 33. Male from Santa Ana near San Jose, San Jose, Costa Rica: 32. Left palp, ventral view; 33. Left palp, retrolateral view. 34, 35. *S. agalenoides*. Female from Santa Ana near San Jose, San Jose, Costa Rica: 34. Vulva, dorsal view; 35. Epigynum, ventral view. Abbreviations: RL, retrolateral lobe of epigynum; CO, copulatory opening.

nating light and dusky bands dorsally. Coxae and trochanters bright orange, conspicuously so on ventral surfaces. Labium and endites dark red-orange with lighter yellowish distal ends. Sternum bright yellow-orange.

Male: Pattern illustrated in Fig. 13. Face reddish brown, black in eye region, with lateral areas (cheeks) lighter orange brown due to clothing of short white setae. Carapace dark reddish brown (mahogany) with lighter, ill-defined submarginal stripes. Pattern of dark lines radiating from thoracic groove (Fig. 13). Dorsum of abdomen brown with dark brown cardiac area and a series of four to five white transverse chevrons diminishing in size posteriorly. Lateral edge of chevrons with white spots (Fig. 13.). Venter tan to pale yellow-brown with slight orange cast. Legs brown with faint dusky bands visible on dorsal surfaces. Coxae and trochanters bright orange on ventral surfaces. Labium and endites darker red orange with lighter splotches at distal ends. Sternum bright orange.

Measurements.—Eight females and two males of *Sosippus placidus*. See Table 2.

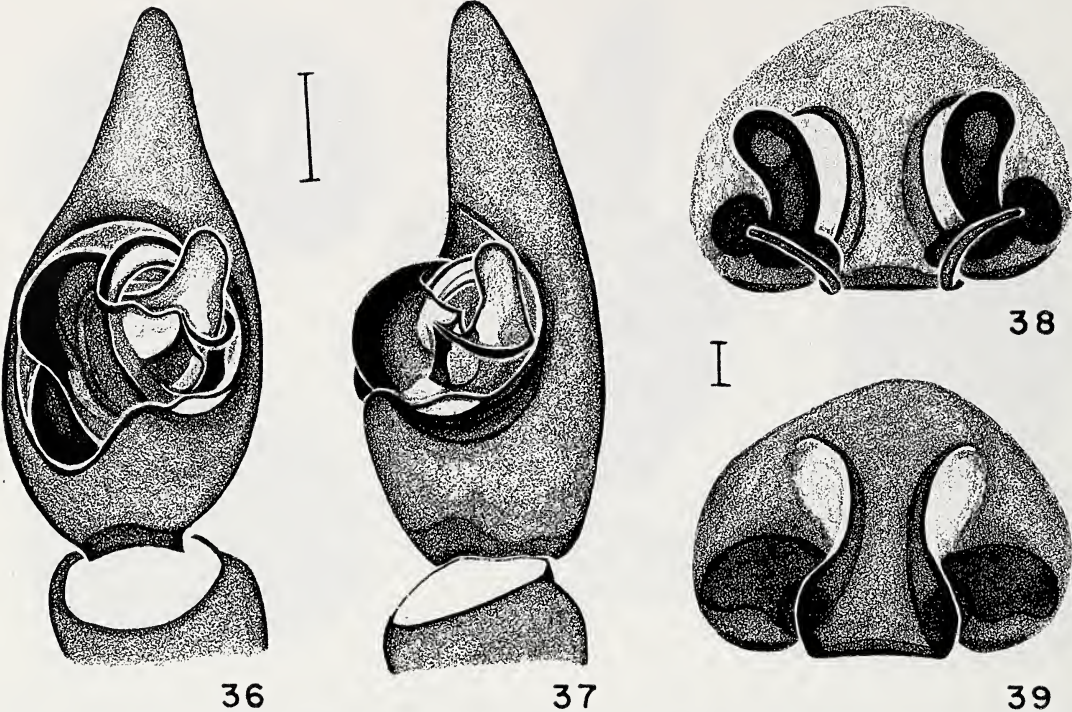
Natural history.—*Sosippus placidus* was collected in a very dry area of scrub vegetation, including *Opuntia* (Brady 1972, figs. 44, 45). This species appears to have different habitat preferences and also apparently a different breeding season than populations of *S. floridanus* in its vicinity. The area where *S. placidus* has been encountered was represented by Red Hill Island during the Aftonian Interglacial (Laessle 1958). Its restricted geographic distribution seems to be directly related to its former insular distribution discussed in the Introduction.

Distribution.—Highlands County, Florida.

Sosippus floridanus Simon 1898

Figs. 4, 26, 40

Sosippus floridanus Simon 1898a:25; Simon 1898b: 323, 325; Banks 1904:121, 135; Comstock 1913: 622; Chamberlin 1908:293; Comstock 1940:639; Wallace 1950:76; Roewer 1955:314; Bonnet 1958:4093; Roewer 1960:1004; Brady 1962:151, figs. 1, 19–20, 40–43; Brady 1972:33, figs. 10–13, 19–24; Platnick 1997:585; Platnick 2006.



Figures 36–39.—*Sosippus agalenoides*. 36, 37. Male from Puntarenas, Puntarenas, Costa Rica: 36. Left palp, ventral view; 37. Left palp, retrolateral view. 38, 39. Female from San Jose, San Jose, Costa Rica: 38. Vulva, dorsal view; 39. Epigynum, ventral view.

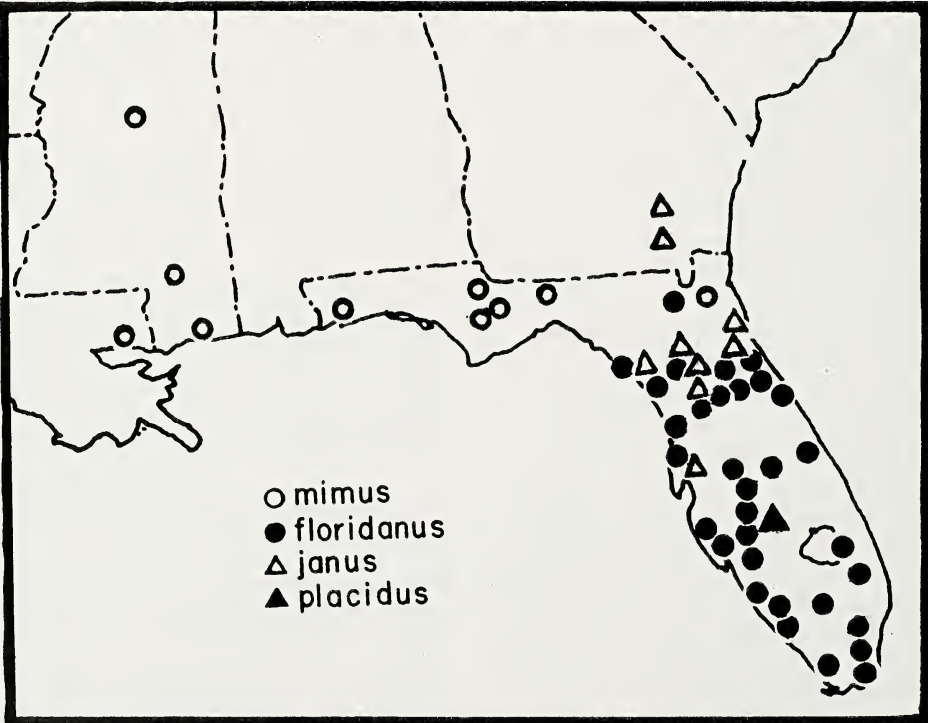


Figure 40.—Distribution map of four *Sosippus* species in southeastern USA.

Table 2.—Dimensions of *Sosippus placidus*.

	Mean (Range)		Mean (Range)
Females (n = 8)			
Anterior eye row	1.71 (1.5–1.9)	Femur I	6.78 (5.7–7.7)
PME width	1.40 (1.2–1.6)	Patella-Tibia I	8.46 (6.9–9.4)
PLE width	2.12 (1.8–2.4)	Metatarsus I	5.19 (4.1–6.3)
POQ length	1.20 (1.1–1.4)	Tarsus I	3.11 (2.7–3.6)
Car. width at PLE	3.71 (3.3–4.1)	Total I	23.54 (19.4–27.0)
Carapace width	5.53 (4.8–6.3)	Femur IV	7.95 (7.3–7.8)
Carapace length	8.01 (6.7–9.1)	Patella-Tibia IV	9.32 (7.8–10.5)
Body length	15.75 (14.2–17.6)	Metatarsus IV	7.85 (6.8–8.9)
Patella-Tibia II	7.95 (7.3–9.0)	Tarsus IV	3.60 (2.9–4.0)
Patella-Tibia III	6.85 (6.0–7.8)	Total IV	28.66 (24.2–31.8)
Males (n = 2)			
Anterior eye row	1.4, 1.6	Femur I	8.0, 8.9
PME width	1.2, 1.3	Patella-tibia I	10.2, 12.2
PLE width	1.8, 1.9	Metatarsus I	7.0, 9.0
POQ length	1.0, 1.0	Tarsus I	4.3, 5.4
Car. width at PLE	2.9, 3.2	Total I	29.5, 35.6
Carapace width	4.6, 6.1	Femur IV	9.3, 10.5
Carapace length	7.0, 9.0	Patella-Tibia IV	11.4, 13.6
Body length	15.1, 16.7	Metatarsus IV	12.2, 13.6
Patella-Tibia II	9.7, 11.4	Tarsus IV	5.1, 6.1
Patella-Tibia III	8.6, 10.2	Total IV	38.1, 43.8

Material examined.—*Type*: USA: *Florida*: female holotype without further locality data, (MNHN), not examined.

Other material: The following are localities not reported in Brady (1962): USA: *Georgia*: Crisp County: 1 ♀, 11.7 km N. of Cordele, 31°58'N, 83°47'W, 30 May 1964, A.R. Brady (HCC). *Florida*: Alachua County: 1 ♀, 24 March 1933, H.K. Wallace (FSCA); 1 ♀, 18 May 1936, H.K. Wallace (FSCA); 1 ♂, Gainesville, 29°39'N, 82°19'W, 2 April 1956, H.V. Weems, Jr. (FSCA); 1 ♂, same location, 23 March 1959 H. V. Weems, Jr. (FSCA); 1 ♂, same location, 7 August 1962, R.E. Woodruff (FSCA); 1 ♀, same location, 19 July 1963, J.F. Anderson (FSCA); Brevard County: 1 ♂, Cocoa, 28°23'N, 80°45'W, 23 February 1936, H.K. Wallace (FSCA); Collier County: 1 ♀, Naples, 26°09'N, 81°48'W, 3 March 1936, H.K. Wallace (FSCA); Dade County: 1 ♂, Everglades National Park, 29 January 1959, H.V. Weems, Jr. (FSCA); 1 ♀, 11.2 km W. of Florida City, 25°27'N, 80°29'W, 31 March 1957, R. Forster, W.J. Gertsch (AMNH); Desoto County: 1 ♂, 2 ♀, Brownville, 27°18'N, 81°40'W, 4 March 1936, Bishop (AMNH); 4 ♂, 9 ♀, Horse Creek, 0.8 km E. of St. Highway 72, 27°13'N, 81°51'W, 12

June 1968, A.R. Brady, J. Toothaker (HCC); Highlands County: 1 ♀, 29 June 1935, H.K. Wallace (FSCA); 2 ♀, Archbold Biological Station, 27°11'N, 81°20'W, 20 June 1962, A.R. Brady (HCC); 3 ♀, Highlands Hammock State Park, 27°30'N, 81°26'W, 19 June 1962, A.R. Brady (HCC); Lee County: 2 ♀, 14 April 1949 (FSCA); Levy County: 1 ♀, 9 April 1937, H.K. Wallace (FSCA); 5 ♂, 6 ♀, Cedar Key, 20°08'N, 83°02'W, 2 June 1964, A.R. Brady, J. Reiskind, P. Tongiorgi (HCC); 5 ♂, 8 ♀, same location, 9 June 1968 A.R. Brady, J. Toothaker (HCC); Marion County: 1 ♂, Ocala National Forest, 27°18'N, 81°22'W, 26 April 1969, H.K. Wallace (FSCA); Pasco County: 6 ♀, Aripeka, 28°26'N, 82°40'W, 2 June 1964, A.R. Brady, J. Reiskind (HCC); 2 ♂, 2 ♀, same location, 13 June 1968, A.R. Brady, J. Toothaker (HCC).

Etymology.—Latin adjective derived from the type locality, the state of Florida.

Diagnosis.—*Sosippus floridanus* is most similar to *S. janus*. *Sosippus floridanus* can be distinguished by the pattern of bold white longitudinal stripes on the carapace (Fig. 4, figs. 34–38 in Brady 1972). In *S. janus* the carapace pattern is more diffuse and there are no distinct longitudinal stripes (Fig. 12, figs. 40,

Table 3.—Dimensions of *Sosippus floridanus* from Cedar Key and Aripeka along the Gulf coast of Florida.

	Mean (Range)		Mean (Range)
Females (n = 10)			
Anterior eye row	1.62 (1.3–1.9)	Femur I	5.71 (4.3–6.7)
PME width	1.41 (1.2–1.6)	Patella-Tibia I	6.89 (5.3–8.3)
PLE width	2.04 (1.6–2.4)	Metatarsus I	4.16 (3.2–5.1)
POQ length	1.24 (1.0–1.4)	Tarsus I	2.70 (2.3–3.2)
Car. width at PLE	3.43 (2.6–4.1)	Total I	19.42 (15.0–23.0)
Carapace width	5.29 (4.0–6.5)	Femur IV	6.53 (5.1–7.7)
Carapace length	7.52 (5.7–8.9)	Patella-Tibia IV	7.78 (6.0–9.0)
Body length	15.20 (11.1–20.2)	Metatarsus IV	6.90 (5.6–8.1)
Patella-Tibia II	6.34 (4.9–7.7)	Tarsus IV	3.26 (2.7–4.0)
Patella-Tibia III	5.71 (4.3–6.7)	Total IV	24.47 (19.3–28.9)
Males (n = 10)			
Anterior eye row	1.28 (1.2–1.4)	Femur I	5.39 (4.8–6.5)
PME width	1.14 (1.0–1.2)	Patella-Tibia I	6.81 (6.2–8.0)
PLE width	1.60 (1.4–1.8)	Metatarsus I	4.14 (3.6–4.9)
POQ length	1.00 (0.9–1.1)	Tarsus I	2.85 (2.5–3.2)
Car. width at PLE	2.43 (2.0–2.8)	Total I	19.01 (17.0–22.6)
Carapace width	4.49 (3.9–5.4)	Femur IV	6.37 (5.6–7.5)
Carapace length	6.24 (5.4–7.1)	Patella-Tibia IV	7.62 (6.7–8.9)
Body length	12.11 (10.4–14.1)	Metatarsus IV	7.28 (6.7–8.8)
Patella-Tibia II	6.41 (5.6–7.6)	Tarsus IV	3.36 (2.9–3.7)
Patella-Tibia III	5.72 (4.9–6.8)	Total IV	24.62 (21.8–28.9)

41 in Brady 1972). The shapes of the epigyna in these two species are similar but consistently different (compare figs. 10–12 with figs. 13–17 in Brady 1972). In *S. floridanus* the edges of the middle field are straight or even (Fig. 26), while in *S. janus* they are indented or scalloped (Fig.27).

Color.—*Female*: Pattern illustrated in Fig. 4 and figs. 35, 37 (Brady 1972). Carapace dark brown, overlaid with black pubescence; black in eye region. Narrow median longitudinal white stripe beginning at second eye row and continuing to the posterior edge of carapace. Broad submarginal white stripes originating at edge of clypeus and running to the posterior edge of carapace. Chelicerae black, lighter orange brown boss on each side. Sternum brownish yellow. Endites and labium reddish brown; lighter at distal ends. Coxae light brownish yellow on ventral surface. Femora gray on ventral surfaces; dorsal surfaces brownish yellow background clothed with white pubescence with narrow gray bands at proximal and distal ends. Remaining leg segments brownish yellow, thickly clothed with black setae. Dorsum of abdomen with reddish brown lanceolate mark at base, en-

closed by a wide black median stripe continuing posteriorly. Two pairs of white spots anteriorly followed by four white chevrons diminishing in size posteriorly. Lateral areas dim brown with scattered black spots. Venter of abdomen grayish brown.

Male: Pattern illustrated in figs. 34, 36 (Brady 1972). The white spots and chevrons on the dorsum of the abdomen are not as conspicuous as in the female, otherwise the coloration and markings are much the same.

Measurements.—Ten females and ten males of *Sosippus floridanus* from Cedar Key and Aripeka along the Gulf coast of Florida. See Table 3.

Natural history.—*Sosippus floridanus* was collected from tubular webs leading under the trunks of Palmetto bushes and into the bases of tufts of high grass in areas of white, sandy soil in several of the High Pine/Palmetto communities that are common through out the Florida peninsula. The webs were often not extensively developed, the tubular portions being hidden and the sheet portion of the web consisting of radiating lines of silk forming a very loose meshwork at the surface rather than a definite sheet. Near Cedar Key we

found large numbers of specimens in extensive sheet webs and tubular retreats made under fallen palm fronds. The ventral surfaces of femora I and II were much darker in many of these specimens than in previous collections examined. Also, the above measurements show these specimens to be somewhat larger on average than the specimens measured by Brady (1962), but within the range of expected variation. Some individuals from the Gulf coast populations exhibit epigyna that are shaped differently than the more common form of *S. floridanus* epigyna, but others have the more common form illustrated previously (Brady 1962, 1972). *Sosippus floridanus*, as presently viewed, is a widespread species in Florida, while other described species are more restricted ecologically and geographically. It is possible that more than one species is represented under this name.

Distribution.—Southern Georgia, throughout peninsular Florida, south to the Florida Keys.

Sosippus janus Brady 1972

Figs. 12, 20–23, 27, 40

Sosippus mimus Chamberlin: Brady 1962: fig. 17 (misidentification, in part, not *S. mimus*).

Sosippus janus Brady 1972: 39, figs. 14–18, 40, 41; Platnick 2006.

Material examined.—*Type*: USA: *Florida*: female holotype, NW. shore of Lake Lochloosa, Alachua County, 29°31'N, 82°08'W, 10 June 1968, A.R. Brady, J. Toothaker (MCZ).

Other material: USA: *Georgia*: Ware County: 1 ♂, 4 ♀, Okefenokee Swamp State Park near Waycross, 29°31'N, 82°08'W, 16 June 1969, A.R. Brady (HCC); 2 ♂, 10 ♀, same location, 3 July 1987, A.R. Brady (HCC). *Florida*: Alachua County: 1 ♀, 14 June 1935, W. Ivie (AMNH); 1 ♀, 13 April 1950, H.K. Wallace (FSCA); 5 ♂, 3 ♀, 2 juveniles, NW shore of Lake Lochloosa, 29°31'N, 82°31'W, 11 April 1968, A.R. Brady, J. Reiskind, J. Toothaker (HCC); 20 ♀, 8 juveniles, same location, 10 June 1968, A.R. Brady, J. Toothaker (HCC); 1 ♂, 1 ♀, 2 juveniles, 4.3 km W. of Melrose, 29°43'N, 82°03'W, 13 June 1968, A.R. Brady (HCC); Hillsborough County: 1 ♀, 4.8 km N. of Mango, 27°59'W, 82°18'W, 10 March 1976, H.W. Levi (MCZ); Levy County: 1 ♂, 2 ♀, 2 juveniles, 20 April 1935, H.K. Wallace (FSCA);

Marion County: 1 ♀, Kerr Park near Lake Kerr, 29°21'N, 81°40'W, October 1956, H.K. Wallace (FSCA); Putnam County: 1 ♀, 2 May 1947, 3 June [year not indicated], H.K. Wallace (FSCA); 2 juveniles, Welaka Reserve, 29°29'N, 81°40'W, 11 November 1974; 4 ♀, same location, 26 May 1978, A.R. Brady (HCC); 1 ♂, same location, 22 May 1981, A.R. Brady (HCC); 1 ♂, 1 ♀, same location, 17 May 1985, A.R. Brady (HCC); 1 ♂, 3 ♀, same location, 16 May 1992, A.R. Brady (HCC); 2 juveniles, same location, 28 April 1993, A.R. Brady (HCC); St. Johns County: 3 ♀, 19.2 km N. of St. Augustine, 29°54'N, 81°19'W, 12 June 1935, H. K. Wallace (FSCA).

Etymology.—The name is a noun in apposition after the Roman god.

Diagnosis.—*Sosippus janus* is most similar to *S. floridanus* in characters of the male palpus and female epigynum, however, it resembles *S. mimus* more in color pattern. The lateral edges of the middle field of the epigynum in *S. janus* are indented or scalloped (Figs. 22, 23, 27), while in *S. floridanus* they are straight (Fig. 26, figs. 10–13, 19–24, Brady 1972). The shoulders or anterior margins below the neck of the middle field in *S. floridanus* are also usually squarer than in *S. janus*. The males can be distinguished by comparing color patterns (compare Fig. 12 with Fig. 4); and descriptions under *S. floridanus*. *Sosippus janus* has 4–4 posterior cheliceral teeth, unlike *S. mimus* which has 3–3 (Brady 1972). Present records also indicate that *S. mimus* does not occur in peninsular Florida.

Color.—*Female*: Pattern illustrated in fig. 41 (Brady 1972). Face dark reddish brown with white setae from ALE to outer lower edge of clypeus. Carapace dark reddish brown with margins of lighter color covered with white pubescence. Alternate dark and white lines radiating from thoracic groove. A median white stripe between PLE to thoracic groove and a pair of white stripes from inner edge of PME continuing to posterior cephalic region. Dorsum of abdomen with a wide dark brown median stripe bounded by lighter areas of brown intermixed with fine white setae. Four or five white chevrons sometimes faintly visible on posterior half. Venter of abdomen pale yellow to yellow brown above epigastric furrow, cream to brown below furrow and thickly clothed with white setae. Legs yellow

Table 4.—Dimensions of *Sosippus janus*.

	Mean (Range)		Mean (Range)
Females (<i>n</i> = 10)			
Anterior eye row	1.66 (1.6–1.8)	Femur I	5.57 (5.0–6.0)
PME width	1.31 (1.2–1.4)	Patella-Tibia I	7.01 (6.5–7.3)
PLE width	1.99 (1.8–2.2)	Metatarsus I	4.12 (3.6–4.5)
POQ length	1.12 (1.0–1.2)	Tarsus I	2.70 (2.6–2.9)
Car. width at PLE	3.67 (3.5–4.0)	Total I	19.40 (18.0–20.5)
Carapace width	5.36 (4.8–5.8)	Femur IV	6.44 (5.7–6.7)
Carapace length	7.62 (6.9–8.1)	Patella-Tibia IV	7.61 (7.0–8.0)
Body length	15.44 (13.7–17.2)	Metatarsus IV	6.72 (6.3–7.0)
Patella-Tibia II	6.50 (6.1–6.7)	Tarsus IV	3.26 (3.0–3.5)
Patella-Tibia III	5.65 (5.3–6.1)	Total IV	24.02 (22.6–25.0)
Males (<i>n</i> = 10)			
Anterior eye row	1.35 (1.2–1.5)	Femur I	5.63 (4.8–6.4)
PME width	1.14 (1.1–1.2)	Patella-Tibia I	7.33 (6.3–8.1)
PLE width	1.66 (1.5–1.8)	Metatarsus I	4.80 (4.0–5.3)
POQ length	0.98 (0.9–1.0)	Tarsus I	3.13 (2.8–3.6)
Car. width at PLE	2.89 (2.4–3.2)	Total I	21.01 (17.8–23.4)
Carapace width	4.81 (4.0–5.9)	Femur IV	6.57 (5.6–7.5)
Carapace length	6.54 (5.7–7.7)	Patella-Tibia IV	7.94 (6.8–8.6)
Body length	12.54 (10.2–14.8)	Metatarsus IV	7.71 (6.7–8.4)
Patella-Tibia II	6.90 (5.7–7.8)	Tarsus IV	3.63 (3.3–4.0)
Patella-Tibia III	6.06 (4.9–6.9)	Total IV	25.82 (22.3–28.3)

brown to orange brown; coxae lighter, yellow orange on ventral surface. Labium and endites dark brown with lighter yellowish distal ends. Sternum yellow-brown.

Male: Pattern illustrated in Fig. 5 and fig. 40 (Brady 1972). Face dark reddish brown with broad white stripes on each side extending from below PME diagonally downward toward cheliceral condyles. Eye region black. Chelicerae dark reddish brown, black distally. Palpus brownish yellow to brown. Carapace reddish brown with three stripes of white setae in cephalic region: a median stripe beginning between PLE and extending to thoracic groove, a pair of white stripes beginning inside PLE continuing diagonally tangent to inner surface of PLE and then straight back to posterior edge of cephalic region. Four pairs of dark lines radiating from thoracic groove. Edge of carapace heavily clothed with white setae, forming an indistinct light marginal stripe. Dorsum of abdomen with broad median brown stripe; lighter laterally and along the sides, mottled brown with white pubescence. Five pairs of white spots at edges of median stripe; the posterior pair sometimes connected, forming a white chevron. Venter of abdomen with broad median yellowish brown stripe

bordered by light brown, clothed with fine white setae. In some cases a pair of thin brown stripes is visible within the broader pale median one. These run lateral to the genital area and converge posteriorly. Labium and endites orange to yellow-brown with distal ends pale yellow to cream. Sternum pale orange to light brownish yellow.

Measurements.—Ten females and ten males of *Sosippus janus*. See Table 4.

Natural history.—*Sosippus janus* is common in the mesic habitats surrounding Lake Lochloosa in Alachua County, Florida, characterized by Live Oak (*Quercus virginiana*) and Spanish Moss (Brady 1972, fig. 43). Since 1972 this species has been collected on numerous occasions at the Welaka Reserve. Here it occurred in moist areas of tall (0.3–0.6 m) herbaceous vegetation growing in roadside drainage ditches, in herbaceous vegetation at the edge of trails cut through pine and mixed hardwood, and in the Live Oak woodland near shoreline along the St. Johns River. At the above two localities adult males were found in mid-April through mid-May, adult females appeared in late April and mid-May and in some abundance by late May and June. Females with egg cases were prevalent in June.

This species matures much earlier than *Rabidosia rabida* and *Hogna ammophila* (Wallace, 1942), two large lycosids occurring in the same habitats. When collecting this species during morning hours at the Welaka Reserve, we found their webs often heavily coated with condensed moisture or dew. As a corollary when *S. janus* was reared in the laboratory, we found that it required considerable moisture to survive. These observations suggest a need for moisture or high humidity by these spiders, and partially explain the restriction of *S. janus* to mesic habitats.

Accompanied by Pat and Gary Miller in July 1987, I had the opportunity to return to Okefenokee Swamp State Park near Waycross, Georgia, where I had collected several specimens of unidentified *Sosippus* in 1969. We found an additional dozen mature specimens in drainage ditches along the roadside in wooded areas. Upon closer examination, these specimens were recognized as *S. janus*. This discovery near Waycross, Georgia, extended the range of this species 240 km northward and again confirmed its occurrence in mesic or moist habitats.

At Welaka Reserve we observed a number of instances of young spiderlings, some obviously representing different instars, living in the funnel retreats and on the platforms of sheet webs with the females. In the laboratory, where we reared specimens in five-gallon aquaria, we observed cooperative feeding by the young spiders on larger prey items, such as crickets. In one case the adult female subdued a large cricket and the young joined in the meal. When we reared spiderlings of *A. georgicola* in 5-gallon (18.9 l) aquaria, we found that they needed to be separated after several instars or only one individual would be found after a couple of days. In the case of *S. janus*, when two individuals were maintained in five gallon aquaria, they remained compatible for four or five instars, usually constructing sheet webs in opposite corners of the container. The feeding regimen was the same in both of these species. In one unusual case a single individual of *S. janus* never made a web of its own but remained near the edge of the web of another spider, presumably subsisting on prey items captured in the common web.

Distribution.—North of the Okefenokee Swamp near Waycross, Georgia to northern Florida; usually in mesic environments.

Sosippus minus Chamberlin 1924

Figs. 5, 24, 25, 40

Sosippus minus Chamberlin 1924:27; Comstock 1940:639; Bonnet 1958:4093; Brady 1962:156, figs. 2, 3, 13–17, 34, 35; Brady 1972:35, figs. 1–9, 2833; Platnick 2006.

Sosippinus minus (Chamberlin); Roewer 1955:313; Roewer 1960:1002.

Material examined.—*Type*: USA: *Louisiana*: Saint Tammany Parish: female holotype, Mandeville, 30°21'N, 90°04'W, 1 May 1921, H.E. Hubert (MCZ).

Other material: USA: *Florida*: Bay County: 1 ♂, 3 ♀, 3 juveniles, 11.2 km S. of Youngstown on US 231, 30°22'N, 85°26'W, 20 June 1968, A.R. Brady, J. Toothaker (HCC); Calhoun County: 1 ♂, Blountstown, 30°27', 85°03'W, 17 April 1938, W.J. Gertsch (AMNH); Escambia County: 2 juveniles, 18 June [year not indicated], H.K. Wallace (FSCA); Jackson County: 1 ♂, 3 April 1953, H.K. Wallace (FSCA); Leon County: 12 ♂, 4 ♀, 5 juveniles, Tall Timbers Research Station, 13 October 1969, June 1970, D.L. Harris (FSCA); Liberty County: 1 ♂, 2–4 June 1952 (HCC); 1 ♂, 5.9 km E. of Torreya State Park, 30°34'N, 84°57'W, 31 May 1964, A.R. Brady (HCC); *Mississippi*. Forrest County: 2 juveniles, Hattiesburg, 31°20'N, 89°17'W, 2–6 January 1942, E.L. Bell (AMNH); Jackson County: 5 ♀, Magnolia State Park near Biloxi, 30°24'N, 88°53'W, 18 June 1968, A.R. Brady, J. Toothaker (HCC); 1 ♂, Ocean Springs, 30°25'N, 88°50'W, 10 May 1931, Dietrich (FSCA); Rankin County: 1 ♂, Thompson field (HCC), 8–12 April, T.C. Lockley (HCC); 1 ♂, same location, 13–15 May 1983, T.C. Lockley (HCC). *Louisiana*: Saint Tammany Parish: 3 ♂, 11 ♀, 1 juvenile, Fountainbleau State Park near Mandeville, 30°21'N, 90°04'W, 17, 18 June 1968, A.R. Brady, J. Toothaker (HCC); 1 ♀, Mandeville, 1 May 1921, H.E. Hubert (AMNH).

Etymology.—The name is a noun in apposition based upon the resemblance (mimicry) of this species to the three species previously described by Simon, *S. mexicanus*, *S. californicus* and *S. floridanus*.

Diagnosis.—*Sosippus minus* is like *S. texanus* in dorsal color pattern and having three

Table 5.—Dimensions of *Sosippus mimus*.

	Mean (Range)		Mean (Range)
Females (n = 10)			
Anterior eye row	1.47 (1.3–1.6)	Femur I	5.23 (4.7–6.0)
PME width	1.24 (1.1–1.3)	Patella-Tibia I	6.61 (5.7–7.5)
PLE width	1.85 (1.7–2.1)	Metatarsus I	3.87 (3.5–4.4)
POQ length	1.07 (1.0–1.2)	Tarsus I	2.51 (2.3–2.9)
Car. width at PLE	3.16 (2.8–3.6)	Total I	18.22 (16.1–20.8)
Carapace width	4.77 (4.2–5.4)	Femur IV	6.18 (5.5–6.8)
Carapace length	6.89 (5.8–8.9)	Patella-Tibia IV	7.33 (6.4–8.4)
Body length	15.16 (10.2–16.4)	Metatarsus IV	6.42 (5.7–7.2)
Patella-Tibia II	6.16 (5.2–7.1)	Tarsus IV	3.13 (2.7–3.6)
Patella-Tibia III	5.43 (4.8–6.1)	Total IV	23.01 (20.2–25.9)
Males (n = 5)			
Anterior eye row	1.40 (1.2–1.6)	Femur I	6.05 (5.3–6.7)
PME width	1.19 (1.1–1.4)	Patella-Tibia I	7.81 (6.7–8.5)
PLE width	1.75 (1.6–2.0)	Metatarsus I	4.88 (4.4–5.2)
POQ length	1.00 (0.9–1.1)	Tarsus I	3.02 (2.8–3.3)
Car. width at PLE	2.79 (2.5–3.1)	Total I	21.75 (19.2–23.7)
Carapace width	4.90 (4.2–5.8)	Femur IV	7.09 (6.3–8.0)
Carapace length	7.18 (5.6–8.4)	Patella-Tibia IV	8.34 (7.3–9.3)
Body length	13.79 (11.1–15.9)	Metatarsus IV	8.11 (7.5–9.0)
Patella-Tibia II	7.51 (6.7–8.2)	Tarsus IV	3.86 (3.5–4.1)
Patella-Tibia III	6.74 (5.9–7.7)	Total IV	27.40 (24.7–30.5)

teeth on each side of the posterior margin of the cheliceral fang groove, however, the structure of the female epigyna is different in these two species (compare figs. 1–9 of Brady 1972 with figs. 21, 22 of Brady 1962). Specimens of *S. texanus* are also larger in average size (compare Table 5 with Table 6). *Sosippus placidus* has 3–3 posterior cheliceral teeth and a similar dorsal pattern, but is easily distinguished by the orange color on the ventral surface of the cephalothorax and abdomen. The structure of the female epigynum in *S. placidus* is also quite distinct (Figs. 18, 19, figs. 25–27 of Brady 1972). Although *S. janus* has a similar dorsal color pattern to *S. mimus*, it has four teeth on each side of the posterior cheliceral groove.

Color.—*Female*: Pattern illustrated in Fig. 5 and figs. 29–31 (Brady 1972). Carapace dark reddish brown or mahogany; darkest in eye region with eyes circled in black. Three longitudinal stripes beginning between PME; consisting of a median stripe continuing posterior to thoracic groove and two lateral stripes passing inside of PME and ending in the cephalic region. These stripes yellowish white in color. No distinct stripe along margins of carapace; diffuse yellowish white setae

instead. Black lines radiating from thoracic groove, accented by very fine yellowish white setae. Chelicerae black, clothed with large black setae, with orange brown boss on each side. Sternum yellowish brown. Labium and endites orange-brown, lighter at distal ends. Leg segments yellowish brown without distinct banding. Ventral surface of femora sometimes having a gray appearance due to heavy clothing of black setae. Dorsal surface of femora clothed with short white setae.

Dorsum of abdomen with a wide brown median stripe from the base of the abdomen to the posterior end, interrupted at intervals. An anterior pair of white spots at lateral edges of median stripe, followed by a series of five white chevrons crossing the median stripe; the ends of the chevrons merging with white spots at the lateral edges of abdomen. Bands of brown dots alternately crossing the median stripe with the chevrons. Lateral areas of dorsum yellowish brown; mottled with darker brown. Venter of abdomen brownish yellow.

Male: Pattern illustrated in fig. 28 (Brady 1972). The pattern in the male is very similar to that of the female described above, except that thick lighter setae along the edges of the

Table 6.—Dimensions of *Sosippus texanus*. Standard deviations of measurements of females made by Brady (1962) were used to calculate 95% confidence limits (C.L.) that are comparable to the ranges listed for other species. Males represent new specimens.

	Mean (C.L.)		Mean (C.L.)
Females (n = 10)			
Anterior eye row	1.79 (1.6–2.0)	Femur IV	7.43 (6.3–8.6)
PME width	1.46 (1.3–1.6)	Patella-Tibia IV	8.86 (7.6–10.1)
PLE width	2.22 (2.0–2.5)	Metatarsus IV	7.30 (6.4–8.2)
POQ length	1.31 (1.2–1.4)	Tarsus IV	3.74 (3.2–4.3)
Carapace width	6.25 (5.3–7.2)	Total IV	27.33 (23.5–31.1)
Carapace length	8.61 (7.3–9.9)		
Body length	17.88 (15.6–20.2)		
Males (n = 5, except *n = 4)			
Anterior eye row	1.73 (1.6–1.9)	Femur I	7.45 (6.9–8.4)*
PME width	1.40 (1.3–1.5)	Patella-Tibia I	9.62 (9.2–10.6)*
PLE width	2.08 (2.0–2.2)	Metatarsus I	6.52 (6.1–7.2)*
POQ length	1.21 (1.1–1.3)	Tarsus I	4.12 (3.9–4.4)*
Car. width at PME	3.81 (3.4–4.2)*	Total I	27.70 (26.1–30.6)*
Carapace width	6.52 (5.8–7.1)	Femur IV	9.18 (8.5–10.1)
Carapace length	8.83 (8.2–9.5)	Patella-Tibia IV	11.04 (10.1–11.8)
Body length	18.04 (16.5–20.1)	Metatarsus IV	10.61 (9.7–11.0)
Patella-Tibia II	9.35 (8.9–10.4)*	Tarsus IV	5.17 (4.7–5.5)
Patella-Tibia III	8.22 (7.6–9.0)*	Total IV	34.61 (33.0–38.4)

carapace often create yellowish white sub-marginal stripes.

Measurements.—Ten females and five males of *Sosippus mimus*. Table 5.

Natural history.—During 17–20 June 1968, Jim Toothaker and I collected *Sosippus mimus* from a substrate of sandy soil in wooded areas and in open fields from eastern Louisiana to western Florida. Like other species of *Sosippus* it occurred commonly in disturbed habitats, for example, fields that had been cleared for construction, fire breaks, and garbage dumps. Tubular retreats were built at an angle into the sides of banks, ruts and furrows. Extending from the tubular part of the web was a sheet or platform. Commonly the tubular portion of the web would lead under a log or other cover in which case it might extend for 9–12 inches (23–30 cm). The posterior end of the tube often appeared to be open, apparently serving as a means of retreat for the spider when disturbed. In cases where the retreat led to a dead-end in a hole or depression, there were side avenues for escape. These webs closely resemble those of *Agelenopsis* species, which also occurred in the same habitat. The specimens of *Agelenopsis* were immature, whereas most of the *S. mimus* were mature and some were carrying egg cases.

The egg case is carried attached to the spinnerets as in other lycosids (fig. 30, Brady 1972).

D. L. Harris, utilizing pitfall traps at Tall Timbers Research Station, recovered immature specimens from 13 October 1969 through 27 April 1970. Males were found in these traps beginning May 4 and continuing until 22 June 1970. Four females appeared in the traps from 11–25 April 1970.

Distribution.—Western Florida to Louisiana (Map 1).

Sosippus texanus Brady 1962
Figs. 6, 41

Sosippus texanus Brady 1962:160; Platnick 2006.

Material examined.—*Type*: USA: *Texas*: Female holotype, Goose Island State Park, Aransas County, 28°01'N, 97°03'W, 15 June 1961, A.R. Brady (MCZ).

Other material: USA: *Texas*: Aransas County: 4 juveniles, Goose Island State Park, 28°01'N, 97°03'W, 7 March 1959, A.R. Brady (HCC); 2 ♂, 2 ♀, same locality, 15 June 1961, A.R. Brady (HCC); Cameron County: 1 ♀, Brownsville, 25°54'N, 97°30'W, 30 November 1934 S. Mulaik (AMNH); Hidalgo County: 4 ♂, 2 ♀, Bentsen State Park, 29 June 1962, A.R. Brady (HCC); 1 ♀, same location, 5 July

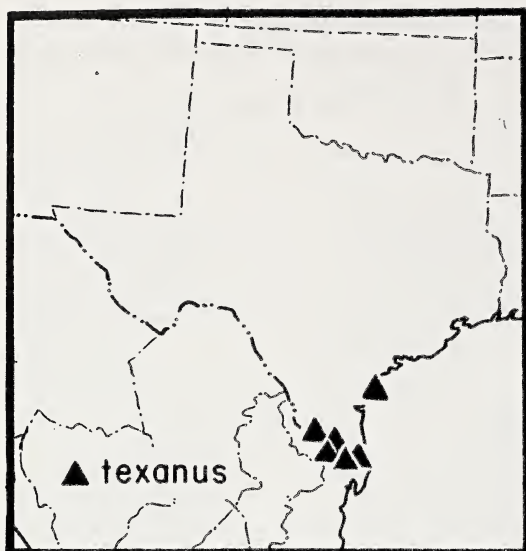


Figure 41.—Distribution map of *Sosippus texanus* in southern Texas and northeastern Mexico.

1972, A.R. Brady, A. Jung (HCC); 1 ♀, Edinburg, 26°18'N, 98°10'W, September–December 1933, S. Mulaik (AMNH); 2 ♀, La Joya, 26°15'N, 98°29'W, 30 October 1938, L.I. Davis (AMNH); 1 ♀, Resaca, 8 km SE. of Brownsville, 25°54'N, 97°30'W, 26 September 1937, L.I. Davis, M. Fones (AMNH); Zapata County: 1 ♀, Lopeno, 26°43'N, 99°07'W, 15 April 1952, Willie (AMNH).

Etymology.—Latin adjective derived from the type locality, the state of Texas.

Diagnosis.—*Sosippus texanus* is close to *S. mimus* in color pattern. *Sosippus texanus* is larger and darker in color with white spots and chevrons on the abdomen that are usually more conspicuous than in *S. mimus* (compare Fig. 6 with Fig. 5). Male palpal organs are similar (compare figs. 37–39 with Figs. 24, 25, and figs. 34, 35 of Brady 1962), but the epigyna are quite distinct (compare figs. 21, 22 to figs. 15, 16 of Brady 1962).

Color.—*Female*: Pattern illustrated in Figure 6. Carapace dark brown covered with black pubescence; black in eye region. Cephalic region of the carapace with three longitudinal white stripes; one median and two lateral ones that pass on the inside of the PLE and end at edge of cephalic region. No well-defined lighter marginal stripes. Sides of cephalic region with a vertical white band behind the clypeus, followed by a black band, then another white band below PLE. Black

lines, accented with white setae, radiating from the thoracic groove. Chelicerae black, clothed with long black setae, conspicuous orange-brown boss on each side. Sternum yellowish brown. Endites and labium dark reddish brown, brownish yellow at distal ends. Ventral surface of coxae yellowish brown. Femora gray-brown on ventral surfaces. White setae on dorsal surface of femora forming alternating bands consisting of proximal gray-brown, white, gray-brown, white, and distal gray-brown. Remaining leg segments dark brown with tarsi and metatarsi darker. Heavy scopulae on tarsus and metatarsus of leg I and II, dark gray in color.

Dorsum of abdomen with a wide brown median strip running the length of the abdomen, with diffuse black setae covering it. Two pairs of white dots at the anterior lateral edges of the stripe; posterior to these a series of six paired white spots connected by white chevrons crossing the brown stripe. Usually the first chevron is represented by two dashes and the arms of the second chevron do not quite join at the midline. Alternating with the white chevrons are bands of darker brown dots. The areas on each side of the median stripe are speckled with tufts of white setae intermixed with dark brown dots on a lighter brown background. Venter light brown.

Male: The pattern in the male is very similar to that of the female. There are fewer black setae over the body and in over-all appearance the male is somewhat more brownish than the female, which appears dark gray or even black.

Measurements.—Ten females and six males. Standard deviations of measurements of females made by Brady (1962) were used to calculate 95% confidence limits (C.L.) that are more comparable to the ranges listed for other species. Males represent new specimens. See Table 6.

Natural history.—*Sosippus texanus* was first collected and observed in the field at Goose Island State Park, a peninsular area of dry sandy soil, characterized by dense stands of Live Oak (*Quercus virginiana*). A few specimens were collected from funnel webs at the base of the trunks of these trees. The sheet or platform part of these webs was not as extensive as those observed in *Agelenopsis*. Most specimens were collected in an area at the edge of a clearing from conspicuous fun-

nel webs with tubular retreats running under logs and into holes in the ground. Again the sheet portions of the web were not highly developed. The emphasis upon the tubular portion of the webs may have been due to their location, especially those webs at the base of trees. During June 1962, *S. texanus* was collected in Bentsen Rio Grande State Park in a campground not far from the banks of the Rio Grande River. Here it was collected at night from tubular webs at the base of concrete posts and hackberry trees. In one case a male was found at the edge of a female's web.

In the field *Sosippus texanus* was observed resting at the mouth of the funnel. The spider rushed forth with great speed to grab insects that touched the radiating lines of silk that formed the sheet portion of the web. The prey consisted chiefly of grasshoppers and ground beetles. Upon grabbing the insect, the spider retreated rapidly into the tubular portion of the funnel, impeding the struggles of the prey. Spiders with retreats that dead-end into a hole or crevice constructed a second short side tube that they utilized for an escape route when disturbed. Most spiders had these secondary tubes angling from the main tube rather than an exit directly to the rear. Several spiders from this locality were reared to maturity and were observed for several months. One spider kept in a cardboard box, provided with a sandy substrate and sticks for a retreat, constructed a funnel web like that found in the field. This web is shown in text fig. 2 of Brady (1962).

Distribution.—Southeast Texas.

Sosippus californicus Simon 1898

Figs. 7, 42

Sosippus californicus Simon 1898a:25; Simon 1898b:324; Banks 1913:182; Comstock 1913:622; Comstock 1940:639; Bonnet 1958:4093; Brady 1962:139, figs. 8, 27, 28, 43, 44; Platnick 1993:508; Platnick 2006.

Sosippus pragmaticus Chamberlin 1924:674 (synonymized by Brady 1962).

Material examined.—Types: *Sosippus californicus*: female holotype, Lower California (MNHN).

Sosippus pragmaticus: MEXICO: Sonora: female holotype, San Carlos Bay (now Bahía de Ohuira), 25°38'N, 108°58'W, 8 July 1921, J.C. Chamberlin (CAS); this material is presumably lost.

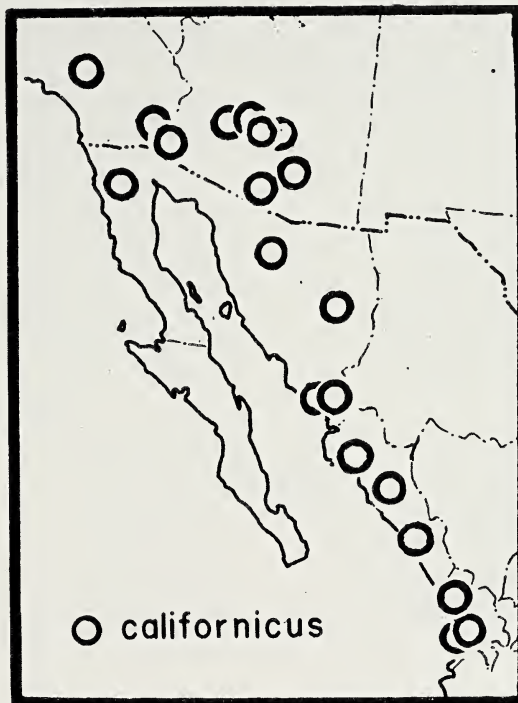


Figure 42.—Distribution map of *Sosippus californicus* in southwestern USA and northwestern Mexico.

Other material (new records): USA: Arizona: Pima County: 4 ♀, Brown's Canyon, Baboquivari Mountains, 31°45'N, 111°31'W, 19 July 1959, V. Roth (AMNH); Pima County: 1 ♂, 2 ♀, 1 juvenile, Sabino Canyon, Santa Catalina Mountains, 32°19'N, 110°49'W, 5 June 1952, M. Cazier, W. Gertsch, R. Schrammel (AMNH); Santa Cruz County: 1 ♀, Pena Blanca Lake, 31°24'N, 111°05'W, 19 May 1963, W.J. Gertsch, W. Ivie (AMNH); Yuma County: 1 ♀, Yuma, 32°44'N, 114°37'W, 15 September 1951, D. Richman (AMNH); 1 ♂, same location, June 1958, V. Roth (AMNH). MEXICO: *Sinoloa*: 1 ♂, 19.2 km S. of Guasave, 25°34'N, 108°28'W, 8 July 1967, R.E. Leech (HCC); 1 ♀, Rosario, 23°00'N, 105°52'W, 15 May 1963, W.J. Gertsch, W. Ivie (AMNH); *Nayarit*: 1 ♀, San Blas, 22°52'N, 105°06'W, 4, 5 August 1947, B. Malkin, C.M. Goodnight (AMNH).

Etymology.—Latin adjective derived from the type locality, the state of California.

Diagnosis.—*Sosippus californicus* resembles *S. agalenoides* and *S. michoacanus* in color pattern. Both *S. agalenoides* and *S. michoacanus* can be separated from *S. californicus*.

Table 7.—Dimensions of *Sosippus californicus*. Standard deviations of measurements made by Brady (1962) were used to estimate 95% confidence limits (C.L.) that are comparable to the ranges listed for other species in this paper.

	Mean (C.L.)		Mean (C.L.)
Females ($n = 38$)			
Anterior eye row	1.62 (1.4–1.8)	Femur IV	7.65 (7.3–8.0)
PME width	1.31 (1.2–1.4)	Patella-Tibia IV	8.86 (8.5–9.2)
PLE width	1.95 (1.9–2.0)	Metatarsus IV	8.26 (7.9–8.6)
POQ length	1.17 (1.1–1.2)	Tarsus IV	3.31 (3.2–3.4)
Carapace width	5.32 (5.1–5.6)	Total IV	28.11 (26.9–29.3)
Carapace length	7.34 (7.0–7.7)		
Body length	16.16 (14.7–17.6)		
Males ($n = 22$)			
Anterior eye row	1.40 (1.4–1.4)	Femur IV	8.02 (7.2–8.9)
PME width	1.19 (1.1–1.2)	Patella-Tibia IV	9.43 (8.4–10.5)
PLE width	1.72 (1.7–1.8)	Metatarsus IV	9.95 (8.9–11.0)
POQ length	1.03 (1.0–1.1)	Tarsus IV	3.76 (3.4–4.1)
Carapace width	5.01 (4.9–5.1)	Total IV	31.16 (30.2–32.2)
Carapace length	6.90 (6.7–7.1)		
Body length	13.92 (13.4–14.4)		

nicus by the structure of the epigynum (compare figs. 27, 28 with figs. 9–30 and 31, 33 of Brady 1962).

Color.—*Female*: Pattern illustrated in Fig. 7. Carapace dark brown with the eye region darkest. Eyes outlined with black. A narrow pale brownish yellow median stripe begins just behind the PME and runs the length of the carapace. Carapace with broad marginal stripes of the same color, both the marginal and median stripes densely clothed with white setae. Marginal stripes broadening anteriorly and extending to edge of clypeus. Chelicerae dark reddish brown, almost black. Sternum brownish yellow. Endites darker reddish brown with distal ends brownish yellow. Proximal segments of legs brownish yellow without distinct contrasting markings; metatarsi and tarsi darker brown.

Dorsum of abdomen with a broad dark brown median stripe from base to tip; two pairs of white spots at lateral indentations of stripe anteriorly, transverse chevrons clothed with white setae posteriorly. Brownish yellow area on each side of median stripe thickly clothed with white setae. Lateral edges of dorsum darker brown, mottled with tufts of white setae. Venter brownish yellow.

Male: Very similar to the female in coloration.

Measurements.—Thirty-eight females and

twenty-two males. Standard deviations of measurements made by Brady (1962) were used to estimate 95% confidence limits (C.L.) that are comparable to the ranges listed for other species in this paper. See Table 7.

Natural history.—Beatty (1961) reported *S. californicus* from riparian woodland formations. These plant associations occur in or adjacent to drainage ways and their flood plains and are characterized by different vegetation than that of the surrounding non-riparian community. This species occurred at varying elevations depending upon the amount of vegetation and moisture available. In the Santa Catalina Mountains it was collected at about 850 meters elev.

Sosippus californicus constructs an expansive sheet web with a central funnel-shaped retreat leading to the base of grassy vegetation, into crevices, or under large rocks. In Sabino Canyon I observed young spiderlings sharing the sheet web with a large female. In Mexico near El Coyote, Sonora this species was collected from webs leading under rocks in a dry stream bed at 1000 meters. A female with egg case was collected from beneath a rock in a canyon filled with Palm trees 26 km. East of Magdalena at 1300 meters elev.

Distribution.—Arizona, southern California, Baja California, south to Nayarit (Fig. 42). Previous locality records for California,

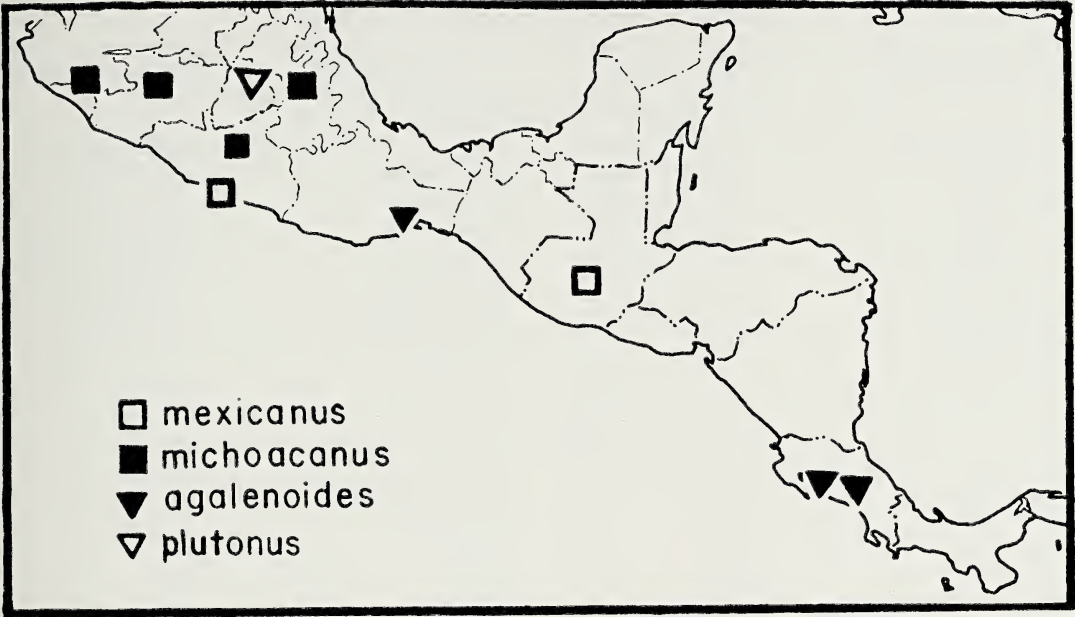


Figure 43.—Distribution map of four *Sosippus* species in southern Mexico and Central America.

Arizona and Mexico are recorded in Brady (1962). New records are listed above.

Sosippus michoacanus Brady 1962
Figs. 10, 14, 28–31, 43

Sosippus michoacanus Brady 1962:148 figs. 7, 31, 32; Platnick 2006.

Material examined.—*Type*: MEXICO: *Michoacan*: Female holotype, Tzararacua Falls, 11 km from Uruapan, 18°55'N, 102°04'W, 14 June 1948, A.M. Davis, L.I. Davis (AMNH).

Other material: MEXICO: *Colima*: 1 ♂, 1 ♀, 12.8 km SW. of Colima, 19°14'N, 103°4'W, 10 May 1963, W.J. Gertsch, W. Ivie (AMNH); *Michoacan*: 2 ♀, Tzararacua Falls, 11.2 km S. of Uruapan, 19°25'N, 102°04'W, 14 June 1948, A.M. Davis, L.I. Davis (AMNH); 1 ♀, same location, 17 June 1964, S. Schlentz (AMNH); *Morelos*: 1 ♀, 4.8 km S. of Cuernavaca, 18°55'N, 99°55'W, 12 July 1963, J.A. Beatty (HCC); *Guerrero*: 1 ♀, Mexcala, 17°56'N, 99°37'W, 2 July 1941, L.I. Davis (AMNH).

Etymology.—Latin adjective derived from the type locality, the state of Michoacan.

Diagnosis.—*Sosippus michoacanus* has an abdominal pattern similar to *S. californicus* (compare Figs. 10, 14 to Fig. 7), but it is much darker in color than *S. californicus* and is

readily recognized by the shape of the epigynum, which has a wide neck and greatly transversely expanded middle field (Figs. 30, 31). The male palpus of *S. michoacanus* is also quite distinct from other species (Figs. 28, 29).

Color.—*Female*: Pattern illustrated in fig. 7 (Brady 1962). Carapace reddish brown, overlaid with black pubescence giving it a darker appearance. Eye region dark brown, almost black, with eyes encircled with black. Thin median stripe beginning some distance behind the third eye row, continuing to posterior edge of carapace. This stripe not conspicuous, with white setae sparsely covering it, densest along the thoracic groove. Broad submarginal stripes extending from clypeus to posterior edge of carapace, clothed with white pubescence. Chelicerae very dark reddish brown, almost black with intermittent, long black setae. Conspicuous boss on each side, light brown. Sternum light brown with gray overtones. Endites and labium reddish brown, yellowish at distal ends. Femora brown dorsally, but with uniformly gray color on ventral surface, forming distinct bands on the lateral and dorsal surfaces. Patellae and tibiae of same color, but with more uniform darker markings.

Dorsum of abdomen with basal reddish

Table 8.—Dimensions of *Sosippus michoacanus*.

	Mean (Range)		Mean (Range)
Females (<i>n</i> = 9, except * <i>n</i> = 5)			
Anterior eye row	1.67 (1.6–2.1)	Femur I	6.17 (5.5–7.3)*
PME width	1.45 (1.4–1.7)	Patella-Tibia I	8.11 (7.3–9.6)*
PLE width	2.13 (1.9–2.6)	Metatarsus I	4.92 (4.3–5.7)*
POQ length	1.22 (1.1–1.4)	Tarsus I	2.98 (2.7–3.5)*
Car. width at PLE	3.70 (3.2–4.6)	Total I	22.02 (19.6–26.1)*
Carapace width	5.41 (4.8–7.2)	Femur IV	7.00 (6.0–8.6)
Carapace length	7.37 (6.5–9.4)	Patella-Tibia IV	8.22 (7.0–10.0)
Body length	15.35 (13.5–21.4)	Metatarsus IV	7.30 (5.6–8.5)
Patella-Tibia II	7.47 (6.7–8.9)*	Tarsus IV	3.03 (2.7–3.9)
Patella-Tibia III	6.49 (5.9–7.8)*	Total IV	25.62 (22.1–30.7)
Male (<i>n</i> = 1)			
Anterior eye row	1.6	Femur I	6.5
PME width	1.4	Patella-Tibia I	8.5
PLE width	2.0	Metatarsus I	6.3
POQ length	1.2	Tarsus I	3.3
Car. width at PLE	3.0	Total I	24.6
Carapace width	5.4	Femur IV	8.0
Carapace length	7.4	Patella-Tibia IV	9.6
Body length	14.8	Metatarsus IV	9.3
Patella-Tibia II	8.2	Tarsus IV	3.7
Patella-Tibia III	7.3	Total IV	30.6

brown lanceolate mark, enclosed by wide dark stripe heavily pigmented with black. Dark brown median stripe bordered by lighter brown area, with lateral regions again becoming dark brown. Venter light yellowish brown.

Male: Pattern illustrated in Fig. 14. Carapace dark reddish brown; eye region black. Thin median stripe present in female, not present in male. Broad white submarginal stripes from clypeus to posterior edge of carapace. Chelicerae dark reddish brown, darkened by fine black setae. Small glossy red-brown boss on each side. Sternum and ventral coxae pale brownish yellow. Labium and endites light brownish yellow with distal ends pale yellow to cream. Femora light brown with gray markings forming bands on dorsal and lateral surface; lighter yellow ventral surfaces. Patellae and tibiae same color, but dusky markings producing indistinct pattern. Metatarsi and tarsi yellowish brown, without darker markings.

Dorsum of abdomen light brown with faint lanceolate cardiac mark; flanked by a white dot and dash on each side within a field of light brown. Three white chevrons posterior to cardiac area. Venter light brownish yellow.

Measurements.—Nine females and one male of *Sosippus michoacanus*. See Table 8.

Distribution.—Colima, Michoacan, Morelos, Guerrero.

Sosippus plutonus Brady 1962
Figs. 8, 43
Sosippus plutonus Brady 1962:150; Platnick 2006.

Material examined.—*Type*: MEXICO: *Distrito Federal*: Female holotype, Tenango del Valle (Tenango de Arista), Mexico City, 19°06'N, 99°36'W, 2400 m elev., 25, 26 August 1946, H. Wagner (AMNH).

Other material: MEXICO: *Distrito Federal*: 1 ♀, 2 juveniles, Tenango del Valle (Tenango de Arista), 19°06'N, 99°36'W, 2400 m elev., 25, 26 August 1946, H. Wagner (AMNH); 2 juveniles, Tenancingo, 2050 m elev., 27 September–7 October 1946, H. Wagner (AMNH).

Etymology.—Latin adjective based upon Greek god of the underworld emphasizing the very dark coloration of this species.

Diagnosis.—The shape of the epigynum of the holotype of *S. plutonus* is similar to *S. californicus*, but the median field is somewhat broader at the base and shorter than in *S. cal-*

Table 9.—Dimensions of *Sosippus plutonus*.

Measurements			Measurements		
Female (<i>n</i> = 1, holotype)					
Anterior eye row	1.3	Femur IV		5.7	
PME width	1.2	Patella-Tibia IV		6.7	
PLE width	1.7	Metatarsus IV		5.8	
POQ length	1.1	Tarsus IV		2.7	
Carapace width	4.3	Total IV		20.9	
Carapace length	6.1				
Body length	11.8				

ifornicus (compare figs. 25, 26 with figs. 27, 28 in Brady 1962). *Sosippus plutonus* (Fig. 8) is also much darker in color than *S. californicus* (Fig. 7). Whether these differences will hold up when more specimens are available remains to be seen. The male of *S. plutonus* is unknown and would probably elucidate this problem.

Color.—*Female holotype*: Pattern illustrated in Fig. 8. Carapace very dark reddish brown with the eye region black. A few white setae along the midline represent the former presence of a thin white median stripe. Broad submarginal stripes, brownish yellow and covered with fine white setae, beginning about the third eye row and continuing to the posterior edge of the carapace. Chelicerae black with lighter colored boss on each side.

Sternum brown. Endites and labium dark brown, lighter at distal ends. Coxae dark gray-

brown on ventral surfaces lighter amber color in proximal regions. More distal leg segments gray-brown with lighter amber color as follows: dorsal paired bands at proximal and distal ends of femora, entire dorsal area of patellae, paired bands at distal ends of tibiae.

Abdomen, which is considerably shriveled, dark brown, almost black, with a series of paired lighter spots as illustrated that are formed from tufts of white setae. Venter brown.

Male: Unknown.

Measurements.—Holotype female. See Table 9.

Natural history.—Presumably *S. plutonus* constructs a funnel web similar to other species in this genus. In 1962 I considered this to be a species distinct from *S. californicus* on the basis of differences in coloration and genital characters. I suggested that it might be a

Table 10.—Dimensions of *Sosippus mexicanus*.

Measurements		Measurements	
Females (<i>n</i> = 2)			
Anterior eye row	1.2, 1.4	Femur IV	5.5, 6.0
PME width	1.0, 1.2	Patella-Tibia IV	6.3, 7.0
PLE width	1.3, 1.7	Metatarsus IV	5.9, 6.5
POQ length	0.9, 1.1	Tarsus IV	2.3, 2.6
Carapace width	3.7, 4.4	Total IV	20.0, 22.1
Carapace length	4.7, 5.7		
Body length	12.6, 13.4		
Male (<i>n</i> = 1)			
Anterior eye row	1.4	Femur IV	7.6
PME width	1.2	Patella-Tibia IV	8.8
PLE width	1.8	Metatarsus IV	8.6
POQ length	1.1	Tarsus IV	3.7
Carapace width	4.6	Total IV	28.7
Carapace length	6.4		
Body length	12.0		

montane species found at extremely high altitude (2400 m) in Mexico. Since no additional adult specimens have appeared in collections, it is possible that this "species" is a high altitude variant of *S. californicus*. Further collections should provide the answer.

Distribution.—Mexico.

Sosippus mexicanus Simon 1888

Figs. 9, 43

Sosippus mexicanus Simon 1888:206; Simon 1898b:325, 327; Pickard-Cambridge 1902:332; Banks 1909:217; Bryant 1948:55; Bonnet 1958:4093; Roewer 1960:1004; Platnick 1997:585; Platnick 2006.

Material examined.—*Type*: MEXICO: female holotype (MNHN).

Other material: MEXICO: *Guerrero*: 2 ♀, Acapulco de Juarez, 16°51'N, 99°55'W, 1 September 1940, H.E. Frizzell (MCZ). *GUATEMALA*: 1 ♂, Sarg (BMNH).

Etymology.—Latin adjective derived from the type locality, the nation of Mexico.

Diagnosis.—*Sosippus mexicanus* is similar to *S. californicus* in the shape of the epigynum (compare figs. 23, 24 with figs. 27, 28 of Brady 1962). They differ distinctly from one another in the dorsal pattern on the abdomen (compare Fig. 9 to Fig. 7). Based upon the limited number of specimens examined, *S. mexicanus* is somewhat smaller than *S. californicus* in total body length. There is no apparent overlap in geographic range of these two species.

Color.—*Female*: Pattern illustrated in Fig. 9. Carapace brown, darker in the eye region with the eyes circled in black. A thin, pale brownish yellow median stripe begins behind the PME row and continues to the posterior edge of the carapace. Broad marginal stripes of this pale color starting at the edge of the clypeus and extending the length of the carapace. The median stripe as well as the marginal ones, clothed with short white setae. Darker brown lines radiating from the thoracic groove, accented with white. Chelicerae dark reddish brown. Sternum brownish yellow. Labium and endites darker reddish brown. Legs brownish yellow without distinct darker markings.

Dorsum of the abdomen with a wide brown median stripe, enclosed by two very light broken lines in the anterior region. Posteriorly the lines are separated into a series of dashes, the

lines and dashes accented with white setae. Lateral to the light lines and dashes the abdomen is brownish yellow mottled with brown. Venter of the abdomen cream colored.

Male: Median longitudinal stripe on carapace not as distinct as in the female. Dorsum of abdomen with a series of paired white spots outlining wide brown median stripe. Male otherwise similar to female in coloration.

Measurements.—Two females and one male.

Distribution.—Guerrero, Mexico and Guatemala. Nathan Banks (1909) reported this species from Costa Rica, but the specimens in question are immature and appear to be *S. agalenoides* also described by Banks from Costa Rica.

Sosippus agalenoides Banks 1909

Figs. 11, 15, 43

Sosippus agalenoides Banks 1909:217; Roewer 1955:313; Bonnet 1958:4093; Roewer 1960:1004; Brady 1962:146; Platnick 1997:585; Platnick 2006.

Material examined.—COSTA RICA: *Puntarenas*: 3 female and 1 juvenile syntypes, Puntarenas, 9°58'N, 84°04'W (MCZ).

Other material: MEXICO: *Morelos*: 1 juvenile, Miactlan, 18°46'N, 99°22'W, 4 October 1942, C. Bolivar (AMNH); *Oaxaca*: 1 ♀, Cerro del Armadillo, 7 January 1948 (AMNH); 1 juvenile, Tehautepec, 16°20'N, 95°14'W, 15 December 1947 (AMNH); 1 juvenile, same locality, 6–10 February 1948, T. MacDougall (AMNH). COSTA RICA: *Alajuela*: 1 ♀, road to Turrazares crossing Rio Alajuela, 10°01'N, 84°13'W, D. Briceno (AMNH); 1 ♀, Finca San Miento near Sialas, 5 February 1976, V.D. Roth, Schroepfer (AMNH); *Puntarenas*: 2 ♀, Puntarenas, 9°58'N, 84°50'W, 1909, P. Biolley (AMNH); San Jose: 4 ♂, 1 ♀, Road to Cartago near San José, 9°89'N, 84°04'W, 19 August 1973, A.R. Brady, R.J. Wolff (HCC); 2 ♂, 2 ♀, Santa Ana near San José, 10°10'N, 85°23'W, 16 July 1994, A.R. Brady, C. Valerio (HCC).

Etymology.—Latin adjective based upon the species resemblance to European genus known by Banks in 1909 as *Agalena* Thorell 1870, which is now considered a junior synonym of *Agelena* Walckenaer 1805 in the family Agelenidae.

Diagnosis.—*Sosippus agalenoides* is most similar to *S. californicus* in color pattern

(compare Figs. 11, 15 with Fig. 7). It can be separated from the latter species by the shape of the epigynum (compare Figs. 38, 39, figs. 29, 30 to figs. 27, 28 of Brady 1962) and the male palpal organ (compare Figs. 36, 37 to figs. 44, 45 of Brady 1962). The epigynum of *Sosippus agalenoides* is also similar to that of *S. mexicanus*, but the former species is much larger in size.

Color.—*Female*: Pattern illustrated in Fig. 11. Carapace light orange-brown, darkest in the eye region. A thin white median stripe begins slightly in front of the third eye row and continues to the thoracic groove. Broad white marginal longitudinal stripes, not as distinct as in *S. californicus*. Lateral edges of the carapace clothed with fine white setae. Chelicerae dark reddish brown, almost black; prominent boss on each side. Sternum light brownish yellow. Endites and labium darker reddish brown; yellowish at distal ends. Proximal leg segments light brownish yellow, metatarsi and tarsi darker reddish brown.

Dorsum of abdomen with a wide brown median stripe beginning at the base and continuing to the spinnerets. The anterior end of this stripe bordered by three white dashes on each side and traversed posteriorly by four to five white chevrons. A series of dark brown dots alternate crossing the dorsum with the white chevron and then continue on each side. Lateral areas of abdomen light brownish yellow, venter lighter, almost cream colored.

Male: Pattern illustrated in Fig. 15. Carapace light orange-brown; eye region dark brown to black. Lighter, thin median stripe, clothed with white setae beginning posterior to PME and continuing to the dark thoracic groove. Broad lighter marginal stripes carpeted with white setae. Chelicerae dark red-brown, almost black, clothed with long white setae. Prominent boss on each side, lighter red-brown. Sternum light brownish yellow. Endites and labium darker brown with cream colored distal ends. Legs light brownish-yellow, with metatarsi and tarsi darker brown. Undersurface lighter with ventral coxae cream colored.

Dorsum of abdomen with a wide brown median stripe from base to spinnerets. Anterior edges of the stripe bordered by paired white dashes and two pairs of white spots, followed posteriorly by four white chevrons. A series of four dark brown dots alternate with

the white chevrons crossing the broad median stripe. Lateral areas of abdomen light brown. Venter cream colored.

Measurements.—Nine females and eight males of *Sosippus agalenoides*. See Table 11.

Natural history.—During a field trip to Costa Rica in 1973, Bob Wolff (Hope College student) and I had unsuccessfully explored a number of habitats that appeared to be similar to those that harbored North American species of *Sosippus*. Then we discovered a hillside on the road from San Jose to Cartago that was heavily populated by *Agave* plants. On many of these plants we found the typical sheet webs of *Sosippus agalenoides* with funnel shaped retreats descending into the bases of these succulent, thorny shrubs. After several spiders had escaped, we learned to capture these spiders by coaxing them onto the platform of the web. Unfortunately only a single female specimen was reared from this collection to compare with earlier specimens described by Nathan Banks from Puntarenas, Costa Rica, in 1909. The males of *Sosippus agalenoides* at this time had not been described, but we had to verify that the coastal species from Puntarenas and those we had captured from the mountainous interior near Cartago were the same species. During a subsequent field trip to Costa Rica in 1994, aided by Carlos Valerio, we were able to locate a population of *Sosippus agalenoides* on a coffee plantation in Santa Ana just to the north of San Jose. Most of these spiders had built their webs in a drainage ditch adjacent to the field of coffee plants. The females of this population appeared to be the same species as that described by Banks (1909). The distribution of *Sosippus* in Costa Rica is much more sporadic than populations encountered in North America.

Distribution.—Morleos, Oaxaca, Mexico to Costa Rica.

ACKNOWLEDGMENTS

Thanks are extended to H.W. Levi and L. Leibensperger (Museum of Comparative Zoology), N.I. Platnick (American Museum of Natural History), G.B. Edwards (Florida State Collection of Arthropods) for the loan of specimens during the various stages of this work. Appreciation is also expressed to colleagues: J.A. Beatty, P. Miller, G. Miller, and C. Valerio, and Hope College students: J. Toothaker,

Table 11.—Dimensions of *Sosippus agalenoides*.

	Mean (Range)		Mean (Range)
Females (<i>n</i> = 9, except * <i>n</i> = 5)			
Anterior eye row	1.90 (1.7–2.1)	Femur I	*7.74 (7.2–8.9)
PME width	1.50 (1.3–1.7)	Patella-Tibia I	*9.66 (8.4–11.0)
PLE width	2.07 (1.9–2.4)	Metatarsus I	*6.04 (5.3–6.8)
POQ length	1.31 (1.1–1.5)	Tarsus I	*3.11 (2.8–3.6)
Car. width at PLE	4.15 (3.6–4.7)	Total I	*26.55 (23.1–29.9)
Carapace width	6.92 (5.6–7.9)	Femur IV	9.15 (7.6–10.1)
Carapace length	9.20 (7.6–10.6)	Patella-Tibia IV	10.45 (8.9–11.4)
Body length	21.05 (17.2–25.0)	Metatarsus IV	8.95 (7.3–9.7)
Patella-Tibia II	*8.80 (7.6–10.0)	Tarsus IV	3.09 (2.7–3.6)
Patella-Tibia III	*7.53 (6.8–8.5)	Total IV	30.72 (26.6–34.0)
Males (<i>n</i> = 8)			
Anterior eye row	1.60 (1.5–1.8)	Femur I	8.11 (7.5–9.3)
PME width	1.28 (1.2–1.5)	Patella-Tibia I	10.35 (9.4–12.0)
PLE width	1.93 (1.8–2.1)	Metatarsus I	6.98 (6.3–8.1)
POQ length	1.08 (0.9–1.3)	Tarsus I	3.36 (2.9–3.7)
Car. width at PLE	3.38 (3.1–3.7)	Total I	28.79 (26.6–33.1)
Carapace width	6.02 (5.6–6.9)	Femur IV	9.19 (8.2–10.5)
Carapace length	7.91 (7.2–9.0)	Patella-Tibia IV	10.69 (9.7–12.1)
Body length	16.23 (14.6–18.6)	Metatarsus IV	10.08 (9.2–11.6)
Patella-Tibia II	9.66 (8.9–11.0)	Tarsus IV	3.67 (3.3–4.0)
Patella-Tibia III	8.42 (8.0–9.6)	Total IV	33.64 (30.5–38.2)

R.J. Wolff and P. Greenstone, who accompanied me on various field excursions in search of *Sosippus*. Research was supported by a Faculty Development Grant from Hope College to A.R. Brady in 1994, and NSF-URP (Undergraduate Research Program) and REU (Research Experience for Undergraduates) grants in 1968, 1973, and 1994. Special thanks go to T. Evans, who assisted with the phylogenetic analyses and cladistic protocols. H.D. Cameron helped to determine the derivation of scientific names. Tom Bultman aided by checking the manuscript for accuracy and consistency.

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Manuscript received 28 January 2006, revised 15 December 2006.

MATING FREQUENCIES OF MALE CRAB SPIDERS, *MISUMENA VATIA* (ARANEAE, THOMISIDAE)

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ABSTRACT. The number of matings obtained by a male is likely to be a major component of his lifetime fitness. Males that depend on finding mates before their competitors must allocate resources to this effort, potentially at the expense of their reproductive rate. Male crab spiders *Misumena vatia* (Clerck 1757) often occur at low densities and experience considerable difficulty in finding females. This constraint might select for their cursorial body form and high movement rates at the expense of their reproductive rate. Male *M. vatia* will not mate more than once in rapid succession and typically no more than once every other day, although they are capable of several matings over their lifetime. Males may rarely encounter virgin females more often than once every other day and thus would experience little loss of fitness from an inability to mate in rapid order.

Keywords: Male fitness, reproductive constraint, scramble competition

The key determinant of male lifetime fitness often is the number of matings a male obtains (Williams 1992). Under many circumstances the difference in number of matings among males is high, reaching its maximum in harem formers, and variance in male fitness is generally taken to be higher than that of females, a consequence of differences between the sexes in investment per offspring. In high-density situations, males may achieve such variance via a dominance hierarchy, which often is size-related (LeBouef 1974; Clutton-Brock et al. 1982). Low-density situations in which male-male contact is the exception provide a situation in which different factors dictate success; here, the first male to find a female may instead be the one to succeed via scramble competition, accompanied by first-male sperm priority (Ghiselin 1974; LeGrand & Morse 2000).

A male should normally maximize the situations in which he can capitalize upon a reproductive opportunity. However, factors other than the ability to mate successively may assume importance. For instance, males that must expend considerable energy and time in finding females may be unable to mate repeatedly, but seldom find themselves in a situation where that ability would provide an advantage. If so, extra allocation to effective movement, even at the expense of failing to

mate females in rapid succession, would provide important benefits at a likely infrequent cost.

Adult male spiders are often assumed to be less common than their females (Foelix 1996), primarily because of an assumed disproportionately high mortality incurred from searching for females (Vollrath & Parker 1992; Shuster & Wade 2003). However, females of many species do not mature simultaneously, with the result that overt competition may nevertheless occur for access to females as they molt into their adult stage, with consequent guarding of penultimate females in many instances. In spite of potential competition, populations with a low number of males relative to females present the opportunity for males, on average, to mate several times.

My crab spider *Misumena vatia* (Clerck 1757) populations exhibit a female-biased primary sex ratio (1.5 females to 1 male), and this ratio shifts to 2.5–5.1 females to 1 male by the adult stage (LeGrand & Morse 2000). Further, adults are not abundant (Holdsworth & Morse 2000) and the males experience considerable difficulty in finding females, which apparently do not emit pheromonal cues (Anderson & Morse 2001; Leonard & Morse 2006), as opposed to other spider species examined in this regard (Tietjen 1977; Elgar &

Schneider 2004). Given this combination of traits, male *M. vatia* should experience strong selection to reproduce multiple times, but the ability to mate in rapid succession would not be under equally strong selection. The number of matings by individual males in my populations is open to question; nevertheless, adult males on average must mate several times in their lifetime, a consequence of the sex ratios of adults noted above (LeGrand & Morse 2000), the extremely high proportion of adult females that produce fertile egg masses (Morse 1994), and the lack of any evidence to suggest that *M. vatia* ever reproduces parthenogenetically (D. H. Morse, unpublished data). The purpose of this study is to establish whether male *M. vatia* will mate in rapid succession and if not, with what frequency they do successfully mate. The results will provide insight into the evolution of this breeding system.

METHODS

Spiders were collected from flowers in fields and along roadsides in South Bristol, Lincoln County, Maine, USA (43.96°N, 69.56°W) during June 1998–2006 and subsequently maintained in 7-dram vials (~26 ml; 5 cm long × 3 cm diameter) until testing. They were fed small moths and flies every other day. All females were collected as penultimates and used as adults within a week after their final molt. Males were collected either as penultimates or adults. Adult males were not mated for the first two days after collection. In all but one experiment individuals were tested within the first week after capture, or the first week after final molt in the case of the penultimates, to insure that their behavior matched that of individuals in the field (Leonard & Morse 2006). In the single exception I repeatedly paired nine males over periods as long as two months to establish how many times they would mate. Matings of *M. vatia* are described in detail in Morse (2007).

To test the ability of an adult male to mate more than once in succession, I first presented him with a recently molted virgin adult female perched on an ox-eye daisy *Chrysanthemum leucanthemum* flower, a frequent hunting site at the time that females molt into the adult stage. Female *M. vatia* readily mate as soon as they have completed their final molt

(Holdsworth & Morse 2000). Five minutes after positioning the female, I released the male onto the flower stem immediately below the flower. Since males almost inevitably move upward in this circumstance (Hu & Morse 2004), they are well positioned to find the female. I observed the male for 30 min after he climbed into the flower, or until he mated with the female. Previous experiments have demonstrated that males not mating within 30 min are unlikely to do so subsequently (Hu & Morse 2004). I ran 28 male-female pairs in this way. Matings usually took 3–10 min, and the males then quickly dismounted the females and retreated a minimum of several body lengths from them (Hu & Morse 2004).

Following these initial runs I presented 14 of the successful males with a second virgin female to determine if they would mate twice in succession. As before I placed the female on a fresh daisy and released the male on the stem of this flower five min later. All second presentations were made within 10 min of the termination of the initial mating.

Any females that these males refused to mate in the first run were then paired with other males that had not mated within the past two days. Any of these males that did not mate with the female presented them in the first run were tested in the same way with a second virgin female, and if they mated with the second female, they were then paired with a third virgin female. Thus all males were given the opportunity to mate twice in succession, and all females that did not mate in their first run were given the opportunity to mate with a second male.

I also further investigated how frequently and how many times males would mate over their adult lifetime. To test frequency, I ran 10 males in the same way as noted above and then repeated the procedure on the following day. I also mated nine other males with virgin females at two-day intervals five to 20 times. Voucher specimens of *Misumena vatia* have been deposited in the American Museum of Natural History, New York.

RESULTS

Twenty-three of 28 males (82.1%) mated with the first virgin female presented them within the 30 min period. All the males that mated inserted both pedipalps one or more times. Of the remaining males, one individual

had still not contacted the female after 30 min, and the remaining four contacted the female but did not mate.

When 14 of the males that mated with the first female were presented with a second virgin female, none of these males would mate with the second females. The difference in their performance in the first and second runs is highly significant (one-tailed sign test, $P < 0.001$). The 14 females used for these second matings were then tested with a new set of adult males. These males mated with all 14 of the females. The performance of the two groups of males with this set of females was highly significantly different ($P < 0.001$, same test).

Four of the five males that did not mate with the first virgin female presented to them proceeded to mate with another virgin female presented to them immediately after the first one, but all five of them refused to mate with a third virgin female that was presented immediately after their second run. The five initially rejected females were eschewed by a subsequent set of males as well, but these last males mated with another set of virgin females presented to them.

All 10 males tested on successive days failed to mate with virgin females on the following day. When I subsequently tested another set of males ($n = 9$) every other day, they mated in 82.5% of the pairings with virgin females (5–20 matings per male, 80 individual runs, 73.7–90.9% acceptance rate), significantly different from the results on successive days ($P < 0.001$ in a Mann-Whitney U -test for independent samples). Since males refused to mate on successive days but usually mated every other day, I conclude that they require a two-day interval between matings.

DISCUSSION

Clearly these male *M. vatia* will not mate twice in rapid succession, or on successive days (but see below), although they will routinely mate every other day. I did not attempt to test them at various intervals between one and two days, but since they are usually diurnal (Morse 1981), even if they could mate at, say, 1.5-day intervals, they would be unlikely to do so in the field.

The second females presented to the males were apparently in no way deficient as mates, so I conclude that the failure of the first set

of males to mate with them resulted from the males' inability to mate twice in rapid succession. The females eschewed by the males in this first test were for some unknown reason unacceptable to all males tested, but the third set of females were likely eschewed by the latter males only because of their apparent inability to mate twice in rapid succession. Thus, the four males that eschewed the first female but mated with the second one should probably be treated as performers rather than nonperformers in this analysis; that is, they mated when presented with the first acceptable female. If so, this correction would change the proportion of male performers to 96.4% (27 of 28).

Mate-choice theory suggests that males should be choosy if presented with an excess of females (see Andersson 1994). Since the average male *M. vatia* in these populations reproduces several times in his lifetime (LeGrand & Morse 2000), one might predict a tendency for choosiness, especially since they do not mate in rapid succession. However, the tendency for males to mate with any available virgin female after a sufficient hiatus bolsters the argument that they do not frequently meet adult virgin females.

The failure to mate in rapid succession would be counterproductive if the males encountered more than one virgin female within a brief period of time. The low population density of these spiders (LeGrand & Morse 2000), combined with the failure of the females to molt simultaneously or to advertise their condition (Anderson & Morse 2001; Leonard & Morse 2006), makes it further unlikely that the failure to mate in rapid sequence constitutes a significant constraint for the males. The average female in this population was not mated until approximately 1.5 days after molting into the adult stage (LeGrand & Morse 2000), although females will readily mate immediately after their last molt (Holdsworth & Morse 2000). Males capable of mating on an every-other-day basis should thus easily account for insemination of all of the females in the population (Morse 1994). However, at this point I do not know whether mating slows a male's subsequent searching rate, nor whether such a slowdown would significantly affect the frequency with which it finds a new female. I also do not know wheth-

er a male needs to recharge his palps before mating a second time.

In spite of the attention paid to the reproductive behavior of spiders, relatively little is known about either the frequency with which males recharge their pedipalps or the mating rates of species that can mate several times. The effect of sperm depletion for multiply mating males is rarely explicitly considered in the literature (Jones et al. 2006). Quantitative data on rates of pedipalp recharging and mating frequencies of spiders appear to be nonexistent. Neither subject is discussed in standard treatises on spider biology such as Savory (1928), Bristowe (1958), Gertsch (1979) and Foelix (1996), though Gertsch (1979) notes without attribution that some species can mate multiple times without recharging their pedipalps, while others have to recharge during mating. Most recent attention to mating rates of male spiders focuses on extreme adaptations in which a male is physiologically or anatomically incapable of mating more than once or twice in its lifetime (e.g., *Tidarren argo*, Theridiidae: Knoflach & van Harten 2001; *Lacrodectus hasselti*, Theridiidae: Andrade and Kasumovic 2005; *Argiope keyserlingi*, Araneidae: Herberstein et al. 2005).

Although it is possible that males failed to mate in rapid succession because they did not have time to recharge their pedipalps with sperm during the experimental period, several lines of evidence suggest that this factor does not explain the failure of these males to mate with a second female in the experiments. First, males almost inevitably refuse to mate again on the day following a mating (no observations in this study and only rare instances in other observations: D. H. Morse pers. obs.). Second, I observed no efforts by the spiders to recharge their pedipalps shortly following a mating in this study. Finally, the males inserted their pedipalps into the females' genital apertures a variable number of times during a mating sequence, so it is unclear whether the males always used up their supply of sperm in the pedipalps. I did not measure sperm loads in the pedipalps because of the limited number of males available for experimentation and their multiple use in these and other experiments.

In addition to the data gathered specifically for this study, I have made it a policy to mate

virgin females used for other studies with males that have not mated the previous day, because I have so seldom obtained matings with males that mated the previous day (D. H. Morse unpubl. data). The males that I ran the largest number of times usually mated on alternate days as long as we could find virgin females for them. Several of these matings produced viable clutches, though in other circumstances I was unable to rear the females to their egg-laying stage before the season ended (D. H. Morse unpubl. data).

It must be reiterated that these males were confined, so that their responses may differ somewhat from individuals in the field. However, I attempted to minimize this effect by testing individuals soon after collecting them. With the exception of the males run multiple times, all males were run within a week of their capture, a period during which confined individuals perform several other acts [foraging (Morse 2000, 2005), line running (Leonard & Morse 2006), orientation and activity (Sullivan & Morse 2004)] similarly to unrestrained individuals in the field.

These males thus form an extreme opposite pole to harem formers (Andersson 1994), although many of them also mate several times under natural circumstances. Harem formers exhibit some of the most extreme examples of sexual dimorphism favoring large males, but these crab spiders are among the most extreme examples of sexual dimorphism favoring small males; although both exhibit a female-biased sex ratio at reproduction (Morse 2007).

ACKNOWLEDGMENTS

I thank J. K. Waage for discussion and K. J. Eckelbarger, T. C. Miller and other staff members of the Darling Marine Center of the University of Maine for facilitating work on the premises. This work was partially supported by the National Science Foundation (IBN-98-16692).

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Manuscript received 28 March 2006, revised 2 November 2006.

A REVIEW OF LEG ORNAMENTATION IN MALE WOLF SPIDERS, WITH THE DESCRIPTION OF A NEW SPECIES FROM AUSTRALIA, *ARTORIA SCHIZOCOIDES* (ARANEAE, LYCOSIDAE)

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ABSTRACT. Morphological modifications of the first pair of legs in addition to widespread color variations of these legs among males of closely related species have been reported in a variety of spiders. Here, the evidence for sexual dimorphism in male foreleg morphology within wolf spiders (family Lycosidae) is reviewed and shown to occur in a number of species belonging to at least seven genera in five subfamilies: *Alopecosa*, *Hogna*, *Schizocosa* (all Lycosinae) *Pirata* (Piratinae), *Evippa*, (Evippinae), *Pardosa* (Pardosinae) and *Artoria* (Artoriinae). These modifications, often in combination with distinct dark pigmentation, can be divided into three major groups: leg elongation, segment swelling and exaggerated setation (“brushes”). The latter two occur mainly on the tibial segment of the first leg. The function of these foreleg modifications has been studied most extensively in the genus *Schizocosa*. Since the courtship displays of all male *Schizocosa* incorporate a seismic component, foreleg ornamentation (namely pigmentation and associated “brushes”) composes only one part of a multimodal courtship display. The function of this foreleg ornamentation appears to vary across closely related *Schizocosa* species and in some instances involves an interaction with the seismic signaling component. In most instances it appears to play a role in female mate choice and/or mate choice learning. In addition to reviewing lycosid foreleg modifications, we describe a new species of wolf spider, *Artoria schizocoides* from southwestern Western Australia that possesses sexually dimorphic modifications of the tibia of the first leg. Unique within the Artoriinae, males of this species carry spatulate setae on the ventral side of the tibia of the first leg that differ morphologically from other leg modifications in wolf spiders.

Keywords: Courtship display, sexual dimorphism, sexual selection, secondary sexual traits

Two main evolutionary processes that work independently or in combination are thought to explain sexual dimorphism or the morphological differences between males and females. One category relates morphological differences between males and females to a reduction in intersexual competition for resources (ecological niche partitioning) (Shine 1989; Fairbairn 1997). The second explains sexual dimorphism by differences between the sexes in the relationship between a particular trait and reproductive fitness (sexual selection or differences in reproductive roles) (e.g., Selander 1972; Hedrick & Temeles 1989; Reynolds & Harvey 1994). Sexual selection arises through competition between members of one sex for reproduction with the other sex. Here, dimorphic structures may either be used in di-

rect aggressive encounters with members of the same sex (generally males; intrasexual selection), or used by members of the opposite sex to assess mate quality (generally females; intersexual selection) (Darwin 1871; Andersson 1994).

In wolf spiders, sexual dimorphism is evident in a multitude of forms and most differences between males and females are attributed to differences in reproductive roles. With a few exceptions (e.g., *Donacosa merlini* Alderweireldt & Jocqué 1991) females are larger than males. In most ground dwelling species, these size differences are mainly explained by a fecundity advantage of larger females (Prenner et al. 1997, 1998, 1999). Sexual dimorphism also exists with respect to differences in trophic morphology (i.e., the sizes of che-

licerae and venom glands); these differences have been ascribed to the increased importance of foraging for females rather than an avoidance of intersexual competition for food (Walker & Rypstra 2001, 2002). Across many wolf spider species, especially those with sedentary females, males also possess comparatively longer legs than females. This leg dimorphism is thought to have evolved through an advantage of more mobile males to encounter females occupying permanent burrows (Framenau 2005a). While the above forms of dimorphism refer mainly to differences in body shape or size, dimorphic color patterns to augment body size and condition have also been argued to play an important role in the mating behavior of wolf spiders (Moya-Laraño et al. 2003).

Dimorphic patterns of foreleg pigmentation appear to be one of the most widespread and conspicuous form of sexual dimorphism among wolf spiders (Framenau, pers. obs.) and these differences in foreleg ornamentation appear to be driven mostly by sexual selection. Male foreleg ornamentation commonly involves extremely dark pigmentation or very distinct light coloration on individual foreleg segments or covering the entire front pair of legs. In some species, males possess an exaggerated form of foreleg ornamentation involving morphological modifications of the first pair of legs. These morphological modifications occur in a variety of forms in most currently recognized subfamilies of wolf spiders. Our study aims to review the evidence for sexual foreleg dimorphism within the spider family Lycosidae by compiling morphological information from the taxonomic literature. In addition, we describe a species with a novel form of male tibial ornamentation—ventral spatulate modified setae. This species, *Artoria schizocoides* n. sp., belongs to the Australasian/Pacific subfamily Artoriinae and is the only species within this subfamily known to the authors with excessive setation on the first pair of legs.

MORPHOLOGICAL MODIFICATIONS IN THE FIRST LEG OF WOLF SPIDERS

Morphological modifications of the first pair of legs in male wolf spiders belong to three major categories: (1) elongation, (2) swelling and (3) exaggerated setation, the lat-

ter two of which are most prevalent on the tibial segment (Table 1).

Elongation.—An elongation of the front pair of legs can be either subtle (e.g., *Alopecosa cuneata* (Clerck 1757) (Kronestedt 1990) or very conspicuous (e.g., *Artoria flavimana* Simon 1909) (Framenau 2002). For example, in the Palaearctic *Alopecosa cuneata*, the ratio of the length of tibia I to tibia IV is higher than in a related species of similar size, *A. pulverulenta* (Clerck 1758) (Kronestedt 1990). This elongation of the forelegs has been related to male courtship displays (Kronestedt 1990), as there is direct contact between the forelegs of a male and female *A. cuneata* in the form of the female grasping the swollen tibial segment of the male with her chelicerae (Kronestedt 1990, for more detail see below). Male *Alopecosa taeniata* (C. L. Koch 1835) also have longer legs as compared to the closely related *A. aculeata* (Clerck 1758) (Kronestedt 1990). In this case however, the elongation is not restricted to the forelegs and increased species-specific mobility of males during courtship is suggested to explain this pattern (Kronestedt 1990), although there is currently no experimental evidence to support this hypothesis.

In almost all wolf spiders the fourth pair of legs is the longest, followed by leg I, and then II and III, or less commonly III and II (expressed in the “leg formula”: $IV > I > II > III$ or $IV > I > III > II$). However, in males of the Australian *A. flavimana* mentioned above, the front pair of legs is extremely elongated and much longer than the fourth pair of legs. In females of *A. flavimana* the fourth leg is the longest, similar to both sexes of all other species in this genus (Framenau 2002, 2004, 2005b, also this study). The elongation is not restricted to a single segment as in *A. cuneata* but concerns all segments. The behavioral mating sequence of *A. flavimana* is not known and therefore the function of this morphological modification remains unclear. In male orb-weaving spiders, an elongation of the first pair of legs has been argued to be beneficial to avoid sexual cannibalism (Elgar et al. 1990).

Swelling.—The tibia of the first leg of male *A. cuneata* is not only elongated (see above) but also distinctly swollen (Fig. 1). The swollen segment does not appear to purely serve to exaggerate a visual signal during male

courtship since the cuticle around the tibia is equipped with numerous pores (Kronestedt 1986, 1990; Dahlem et al. 1987). The pores correspond to exocrine glandular units which are composed of a large adenocyte, a long sinuous epicuticular ductile and a canal cell among supporting epidermal cells (Juberthie-Jupeau et al. 1990). During courtship, the female has to actively grasp one tibia of the male with her chelicerae before he can mount her. During this grasping it is possible that females are able to assess secretions from the male's gland tissue (Dahlem et al. 1987). A swelling of the tibia of the first leg is also evident in *Pirata cantralli* Wallace & Exline 1978 and *Pardosa vancouveri* Emerton 1917 (Dondale & Redner 1990), and described as "slight" for *A. pulverulenta* (see Dahlem et al. 1987), suggesting a similar morphology and function (Table 1). Scattered pores have also been found on legs of other lycosids, e.g., in *Pardosa* C. L. Koch 1847, *Trochosa* C. L. Koch 1847 (Kronestedt 1986), and *Acantholycosa* Dahl 1908 (Kronestedt & Marusik 2002) and in *Xerolycosa miniata* (C. L. Koch 1834) (Juberthie-Jupeau et al. 1990).

Color dimorphism and excessive setation ("brushes").—The most conspicuous sexual dimorphism in wolf spiders involves differences in foreleg pigmentation between the sexes, with males possessing dark pigmentation on particular foreleg segments. In some species this pigmentation is accompanied by the addition of dense brushes of specialized setae. Male pigmentation/brushes are often referred to as secondary sexual ornamentation and are thought to play an important role in reproductive behavior. The function of male foreleg ornamentation has received a great deal of attention within the Nearctic species of the genus *Schizocosa* where 14 of the 24 described species in North America display foreleg dimorphisms (Stratton 2005). The dimorphisms of some species are considered "slight" (Stratton 2005) and original species descriptions state that the "general structure and color" of females is "essentially as in males" (*S. floridana* Bryant 1934, *S. maxima* Dondale & Redner 1978, *S. saltatrix* (Hentz 1844)). Without considering these species, four North American species remain that possess foreleg pigmentation only: one species with pigmentation on the tibia (*S. uetzi* Stratton 1997) and three species with pigmentation

on the femur (*S. cespitum* Dondale & Redner 1978, *S. communis* (Emerton 1885), *S. retrorsa* (Banks 1911)) (Stratton 2005). Seven North American species are described as having brushes on their foreleg tibia: four species with tibia I brushes and pigmentation (*S. aulonia* Dondale 1969, *S. bilineata* (Emerton 1885), *S. salsa* Barnes 1953, *S. segregata* Gertsch & Wallace 1937; Table 1) and three species complexes with tibia I brushes and pigmentation in addition to femur I pigmentation (*S. crassipes* (Walckenaer 1837) (Fig. 2), *S. ocreata* (Hentz 1844), *S. stridulans* (Stratton 1984; Table 1) (Stratton 2005). Based upon a morphological phylogeny of the North American species, male foreleg ornamentation is suggested to have evolved independently five to six times and to have been subsequently lost two or three times (Stratton 2005).

All known *Schizocosa* species possess a seismic component to their courtship display and seismic signaling is believed to be ancestral in this genus (Stratton 2005). A survey across wolf spiders found male foreleg ornamentation to be associated with the presence of active leg-waving displays, resulting in the suggestion that all ornamented species possess multimodal courtship signaling (seismic and visual) (Hebets & Uetz 2000). In signal isolation experiments across numerous *Schizocosa* species, which vary in presence or absence and type of foreleg ornamentation, females of only brush-legged species responded to isolated conspecific visual signals while females from all species responded strongly to conspecific male seismic signals (three monomorphic species: *S. duplex* Chamberlin 1925 (Hebets & Uetz 1999); *S. rovneri* Uetz & Dondale 1979 (Scheffer et al. 1996); *S. saltatrix* (Uetz & Roberts 2002); one pigmentation only species: *S. uetzi* (Hebets & Uetz 1999); and three brush-legged species: *S. crassipes*, *S. stridulans* (Hebets & Uetz 1999), and *S. ocreata* (Scheffer et al. 1996); summarized in Uetz & Roberts 2002; Hebets & Papaj 2005). These results suggest that while seismic signaling is important across all species, visual signaling is putatively important in species with strong sexual foreleg dimorphism.

The foreleg brushes in *S. ocreata* are known to be condition-dependent (Uetz et al. 2002) and in the absence of seismic signals,

Table 1.—Morphological modifications of legs in male wolf spiders. Abbreviations: pt = patella; tb = tibia; t = tarsus, mt = metatarsus. Roman numbers refer to leg (e.g., I = leg 1).

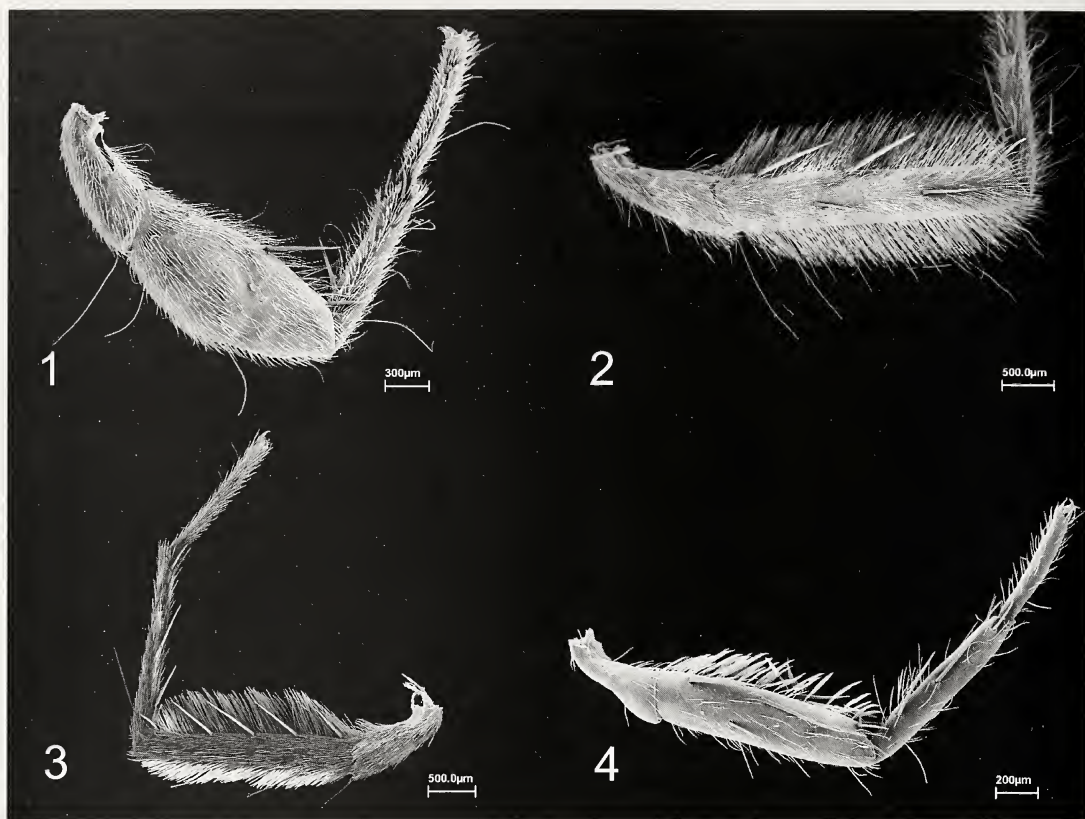
Species	Distribution (Platnick 2006)	Morphological modification of legs	Reference
Piratinae (sensu Zyuzin 1993)			
<i>Acantholycosa solituda</i> (Levi & Levi 1951)	Nearctic (Rocky Mountains)	tb and mt I and II with dense cover of lanate pubescence of long, light, curved, fine setae	Kronestedt & Marusik (2002, fig. 14)
<i>A. sternerii</i> (Marusik 1993)	Palearctic (Mongolia, Sth Siberia)	tb and mt I and II with dense cover of lanate pubescence of long, light, curved, fine setae	Kronestedt & Marusik (2002, figs 15, 16)
<i>Pirata canadensis</i> Dondale & Redner 1981	Canada	t of leg I curved	Dondale & Redner (1990, fig. 371)
<i>P. cantralli</i> Wallace & Exline 1978	USA, Canada	tb I & mt I swollen, mt I with many long curly setae ventrally	Dondale & Redner (1990, fig. 375)
Lycosinae (sensu Dondale 1986)			
<i>Alopecosa cuneata</i> (Clerck 1757)	Palearctic	pt I & II slightly swollen, tb I extremely swollen and slightly elongated, tb II slightly swollen	Fig. 1; Dahlem et al. (1987, figs. 1c, 3, 4), Kronestedt (1986, fig. 1), Kronestedt (1990, fig. 13H)
<i>A. pulverulenta</i> (Clerck 1757)	Holarctic	pt & tb I & II slightly swollen	Dahlem et al. (1987, fig. 1b) (doubtful as per T. Kronestedt, pers. comm.)
<i>A. barbipes</i> (Sundevall 1833)	Palearctic	tb and mt I with ventral brushes	Dahlem et al. (1987, fig. 1d)
<i>Camptocosa parallela</i> (Banks 1898)	Southern USA, Mexico	tb and basal half of mt I with long dense black setae	Dondale et al. (2005)
<i>C. texana</i> Dondale, Jiménez & Nieto 2005	Texas (USA)	tb and basal half of mt I with brush of long dark setae, more dense dorsally and ventrally	Dondale et al. (2005)
<i>Hogna crispipes</i> (L. Koch 1876), <i>H. kuyani</i> Framenau, Gotch & Austin 2006, <i>H. diyari</i> Framenau, Gotch & Austin 2006	Australia, Pacific	mt I with thin, hair-like setae around whole circumference	Framenau et al. (2006)
<i>Schizocosa aulonia</i> Dondale 1969	USA	tb I with brushy setae	Dondale (1969), Stratton (2005, fig. 23)
<i>S. bilineata</i> (Emerton 1885)	Nearctic	tb I with brush of erect black setae	Dondale & Redner (1990), Stratton (2005, fig. 25)
<i>S. crassipes</i> (Walckenaer 1837)	USA	tb I with brush of erect black setae	Fig. 2; Stratton (2005, fig. 27)

Table 1.—Continued.

Species	Distribution (Platnick 2006)	Morphological modification of legs	Reference
<i>S. ocreata</i> (Hentz 1844) (varying morphospecies differentiated in Stratton (2005)	Nearctic	tb I with brush of erect black setae	Dondale & Redner (1978, fig. 5), Dondale & Redner (1990, fig. 50), Stratton (1991, fig. 11; 2005, fig. 29–31)
<i>S. salsa</i> Barnes, 1953	USA	tb I with apical brush of erect black setae	Stratton (2005, fig. 24)
<i>S. segregata</i> Gertsch and Wallace 1937	USA	tb I with brushy setae mainly ventrally	Stratton (2005, fig. 26)
<i>S. stridulans</i> Stratton, 1984	USA	tb I with brushy setae	Stratton (1991, fig. 13; 2005, fig. 28)
Pardosinae (sensu Dondale 1986)			
<i>Pardosa agrestis purbeckensis</i> F.O. P.-Cambridge 1895	Western & Central Europe	t, mt & apical part of tib I with long, rigid, straight setae	Tongiorgi (1966b, fig. 21), Heimer & Nentwig (1991, fig. 860.2)
<i>P. astrigera</i> L. Koch 1878	Palaeartic	tb and mt I with many long, straight setae	Tanaka (1993)
<i>P. ilguensis</i> Nosek 1905	Turkey	tb & mt I & II slightly swollen and covered with short setae, scopulous ventrally	Tongiorgi (1966b, fig. 20)
<i>P. mixta</i> (Kulczyn'ski 1887)	Palaeartic	t, mt & apical part of tb I with very long lateral and forwardly directed setae	Tongiorgi (1966a, fig. 106; 1966b, fig. 23); Heimer & Nentwig (1991, fig. 859.5)
<i>P. plumipes</i> (Thorell 1875)	Palaeartic	tb & mt I with very long hair-like setae	Tongiorgi (1966b, fig. 22)
<i>P. vancouveri</i> Emerton 1917	USA, Canada	mt & t I swollen	Vogel (2004, fig. 127)
<i>P. vittata</i> (Keyserling 1863)	Europe to Georgia	mt II with ventrally with long setae	Tongiorgi (1966a, fig. 6)
Evippinae (sensu Zyuzin 1985)			
<i>Evippomma plumipes</i> (Lessert 1936)	Africa	tb I with plumose setae, mt I densely covered with white setae	Alderweireldt (1992)
<i>E. squamulatum</i> (Simon 1898)	Africa	tb I with plumose setae	Fig. 3; Alderweireldt (1992, fig. 1d)
Artoriinae (sensu Framenau 2007)			
<i>Artoria flavimana</i> Simon 1909	Australia	extremely elongated front leg	Framenau (2002)
<i>A. schizocoides</i> n. sp.	Western Australia (this study)	ventral brush of spatulate setae	Fig. 4

females have decreased receptivity to males with shaved versus intact brushes (Scheffer et al. 1996) as well as to males with smaller brushes (McClintock & Uetz 1996). Curiously, female receptivity did not vary with male

ornamentation in experiments using the video playback technique, with courtship sequences involving manipulated male ornamentation (“control” video vs “no ornamentation” video vs “enhanced brushes” video; McClintock



Figures 1–4.—Photographs of ornamented tibia on the first pair of legs in male wolf spiders. 1. Tibial swelling in male *Alopecosa cuneata* from Marburg, Germany (WAM T56440). 2. Tibial setae in male *Schizocosa cf. crassipes* from Oxford Campus, University of Mississippi, USA (WAM T56106). 3. Tibial setae in male *Evippomma squamulatum* from Tuinplaas, Springbokvlakte, South Africa (WAM T56480). 4. Tibial setae in male *Artoria schizocoides* from Jarrahdale, Western Australia (WAM 97/584).

& Uetz 1996). Live trials involving males with shaved brushes versus intact brushes also did not result in mating frequency differences (Scheffer et al. 1996). Ultimately, tibia I brushes in *S. ocreata* are thought to increase courtship signal efficacy in a seismically unpredictable, heterogeneous signaling environment (Scheffer et al. 1996). A pre-existing bias in females for foreleg brushes was previously suggested to have played a role in the evolution of *S. ocreata* foreleg ornamentation (McClintock & Uetz 1996); however a recent morphological phylogeny suggests that the formerly observed preference of females from a non-ornamented species (*S. rovneri*, McClintock & Uetz (1996)) for males with brushes is a retained behavioral trait (Stratton 2005).

In experiments using the video playback technique in the absence of seismic signals,

females of a second brush-legged species, *S. crassipes* showed a marginally significant preference for pigmented males over non-ornamented males (Hebets & Uetz 2000), suggesting a role of brushes in female mate choice. Females of a third brush-legged species, *S. stridulans*, were significantly more receptive to video playbacks of males with enhanced brushes as compared to males with pigmentation removed (Hebets & Uetz 2000), clearly demonstrating a role of foreleg ornamentation in female mate choice. However, in a follow-up study using the same video playbacks in conjunction with seismic courtship signals from live males, female *S. stridulans* did not distinguish among visual stimuli (Hebets unpublished data), suggesting that visual signals are important only in the absence of seismic information for *S. stridulans*. Interestingly, the exact opposite pattern was ob-

served in a pigmentation only species (*S. uetzi*), where females did not distinguish among visual stimuli using video playbacks in the absence of a seismic signal (Hebets & Uetz 2000). However, with the addition of a conspecific seismic signal, females preferred males with exaggerated ornamentation (“brushes added” vs “no ornamentation” video, Hebets 2005). Follow-up experiments with *S. uetzi* suggest that the seismic and visual signals interact such that the seismic signal alters a female’s visual attention (Hebets 2005). A recent study using live manipulated males questions the significance of this inter-signal interaction for inexperienced females (Hebets et al. 2006) but suggests that the pigmentation observed in *S. uetzi* may be important in female mate choice learning. The importance of early experience on adult mate choice was previously demonstrated in *S. uetzi* as females were more likely to mate with a male of a familiar versus unfamiliar foreleg pattern (Hebets 2003). In the same study, females were more likely to cannibalize males possessing an unfamiliar foreleg pattern, suggesting strong selection on male ornamentation, maturation time, and/or male behavior (Hebets 2003).

While the tibia I brushes of many *Schizocosa* species have attracted much scientific attention, such morphological modifications are also found in other genera within the subfamily Lycosinae Sundevall 1833 (sensu Dondale 1986) (Table 1). *Alopecosa barbipes* (Sundevall 1833), for example, was listed as junior synonym of *A. accentuata* (Latreille 1817) by Lugetti & Tongiorgi (1969), and the presence (*A. barbipes*) or absence (*A. accentuata*) of tibial brushes was previously regarded as intraspecific variation. Subsequently, *A. barbipes* was removed from this synonymy based on morphological, behavioral and ecological differences (Dahlem et al. 1987; Cordes & Helversen 1990) and recent molecular studies confirmed the identity of *A. barbipes* as a separate species (Vink & Mitchell 2002). Bushy setae on the first tibia of males can also be found in other subfamilies of wolf spiders (Table 1). Two species of *Evippomma* Roewer 1959, *E. plumipes* (Lessert 1936) and *E. squamulatum* (Simon 1898), carry a striking fringe of black setae on the ventral and dorsal side of the first tibia (Fig. 3; also Alderweireldt 1992). The males of *Artoria schizocoides* n.

sp. carry unique spatulate setae on the ventral side of their first tibia (Fig. 4; see also below). Other segments in addition to the tibiae may carry conspicuous modified setae. The males of *Pirata cantralli* Wallace & Exline 1978 have long curly setae on the metatarsi of the front legs (Dondale & Redner 1990). Some species of *Pardosa* C.L. Koch 1847 have conspicuous setae on the tarsi, metatarsi and tibia (Tongiorgi 1966a, b). Although a similar function as in *Schizocosa* is likely, there is no experimental evidence on the significance of these structures in these species.

The excessive setation observed in some wolf spider species may not function solely in a reproductive context. For example, in some Australian species currently listed in *Hogna* Simon 1885 males possess very fine, long setae around the whole circumference of the front tibia (Table 1; also Framenau et al. 2006). In contrast to the setation in *Alopecosa*, *Schizocosa*, *Evippomma*, *Pardosa* and *Artoria*, these setae are less conspicuous in live specimens and thus a role in visual signaling appears doubtful. When disturbed, males run with their front legs raised high in the air, suggesting a putative role in sensory perception and information gathering (Framenau pers. obs.). However, there is currently no experimental evidence for this function and detailed studies of setae structure may elucidate a putative role in sensory perception.

In summary, morphological modifications of the front legs in wolf spiders can be found in most of the currently recognized subfamilies (Dondale 1986; Zyuzin 1993; Framenau 2007). They are generally absent in the larger, burrowing and mainly nocturnal species, for example in the genera *Lycosa* Latreille 1804 (Palearctic) (e.g., Orta-Orcaña et al. 1996), *Geolycosa* Montgomery 1904 (Nearctic, Palearctic), *Tasmanicosa* Roewer 1959 and *Venatrix* Roewer 1960 (e.g., Cutler 2002) (both Australian). It appears that foreleg modifications are more common in smaller, diurnal species, which strengthens their putative function in visual signaling. Although numerous *Schizocosa* species have been the focus of elegant studies regarding female mate choice and the evolution of male foreleg dimorphism/ornamentation, much remains to be learned. Foreleg ornamentation appears to function in different ways even among closely related *Schizocosa* species, suggesting that it may be

difficult to make broad generalizations about the evolution of sexual dimorphisms in wolf spiders. However, studies of similar morphological modifications in other wolf spider taxa are needed and will certainly add to our general understanding of the evolution of sexual foreleg dimorphism.

TAXONOMY

Artoria is an Australasian genus, currently with 23 representatives from the Philippines in the North to New Zealand in the South (Framenau 2002, 2004, 2005b; Framenau et al. 2006). However, a large number of unnamed species have been found in Australian and Pacific collections and the genus is believed to include more than 80 species in Australia alone (Framenau, personal observation). *Artoria* is characterized by a male pedipalp with a bifurcate or spoon-shaped apically directed tegular (= median) apophysis with a narrow base (Framenau 2002). Recent molecular studies suggest that *Artoria* as currently defined may not represent a monophyletic group (Murphy et al. 2006), however all currently described *Artoria* species belong to the Australasian/Pacific subfamily Artoriinae that received very good nodal support (Vink et al. 2002; Murphy et al. 2006). This subfamily can easily be identified by the presence of a basoembolic apophysis in the male pedipalp (Framenau 2007). Other genera within this clade include *Anoteropsis* L. Koch 1877 and *Notocosa* Vink 2002 (Vink 2002), *Tetrallycosa* Roewer 1960 (Framenau et al. 2006) and *Diahogna* Roewer 1960 (Framenau 2006).

METHODS

Descriptions are based on specimens preserved in 70% EtOH. A female epigynum was prepared for examination by submersion in lactic acid for 24 h. Scanning electron microscope (SEM) images were taken with a Carl Zeiss Leo 1420VP (Oberkochen, Germany) after fixing the respective spider parts in Karnovsky's fixative (Sheehan & Hrapchak 1980) and osmic acid. For clarity, the illustrations of genitalia omit the setae. The morphological nomenclature follows Framenau (2002). All material investigated is lodged at the Western Australian Museum, Perth, Australia (WAM).

Abbreviations.—Measurements are in mm: total body length (TL), carapace length (CL) and width (CW), abdomen length (AL)

and width (AW). Eyes: anterior row of eyes (AE), anterior median (AME), anterior lateral (ALE), posterior row of eyes (PE), posterior median (PME), posterior lateral (PLE).

Artoria schizocoides new species

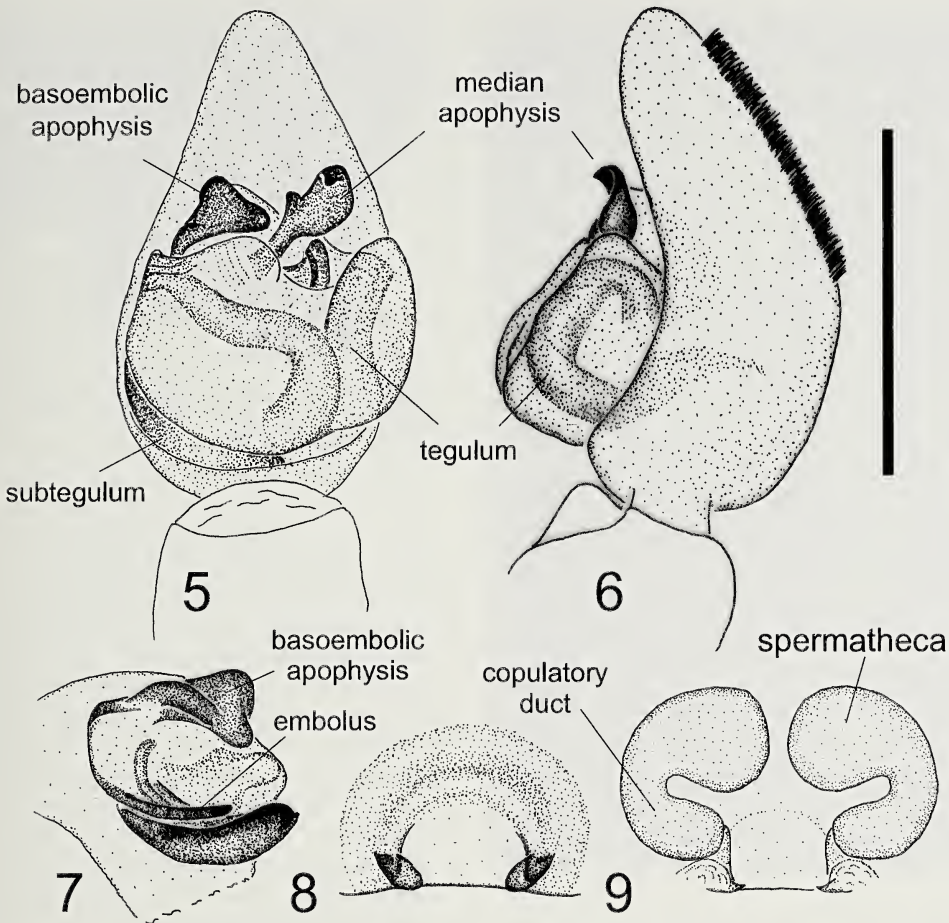
Figs. 4–11

Types examined.—Holotype male, Australia, Western Australia: Bluff Knoll, Stirling Range National Park, 34°23'S, 118°15'E, 19 March 1996, S. Barrett, site 230, wet pitfall trap (WAM T53800). Paratypes: 1 male, 4 females, Bluff Knoll, Stirling Range National Park, Western Australia, Australia (34°22'56"S, 118°14'55"E), 7 September 1995, S. Barrett, site 214, 900m, pitfall traps (WAM T53799, T53875).

Other material examined.—AUSTRALIA: *Western Australia*: 1 ♂, 1 ♀, Alcoa mine, NE Jarrahdale, 32°17'S, 116°08'E (WAM T44717); 2 ♂, Alcoa mine site & forest, N and NW Jarrahdale, 34°54'S, 117°55'E (WAM 97/583–4); 51 ♂, 10 ♀, Dwellingup, 32°43'S, 116°04'E (WAM T42134, T53762–76); 1 ♂, Forth River, 45 km SE Northcliffe, 34°50'S, 116°26'E (WAM T65102); 1 ♂, 1 ♀, Jarrahdale, 32°20'S, 116°03'E (WAM T55764–5); 7 ♂, 2 ♀, Manjimup, 32°15'S, 116°09'E (WAM T53777–9); 15 ♂, 4 ♀, Mt. Cooke, 32°25'S, 116°18'E (WAM 98/2168, T53780–2, T62483, T65097; T65595); 60 ♂, 3 ♀, Mt. Lindesay, 34°50'30"S, 117°18'21"E (WAM T53807–10); 3 ♂, 1 ♀, Porongurup National Park, 34°40'56"S, 117°51'59"E (WAM T53805); 1 ♂, Quinninup, nearby, 34°26'S, 116°15'E (WAM T65093); 21 ♂, 4 ♀, Stirling Range National Park, Bluff Knoll, 34°23'S, 118°15'E (WAM T53799, 53801–3); 3 ♀, 4 juv., Stirling Range National Park, 12 km S Bluff Knoll, 34°29'S, 116°15'E (WAM T55578); 1 ♂, Stirling Range National Park, Mondurup Peak, 34°24'18"S, 117°48'44"E (WAM T53804); 29 ♂, 14 ♀, 7 juveniles, Stirling Range National Park, S face of Pyongurup Peak, 34°22'17"S, 118°19'20"E (WAM T53761); 1 ♂, 1 ♀, Stirling Range National Park, The Cascades, 34°22'29"S, 118°14'17"E (WAM T53832); 1 ♂, Sues Bridge, 50 km SW Nannup, 34°05'S, 115°40'E (WAM T65136).

Etymology.—The specific name is an adjective in apposition and refers to the wolf spider genus *Schizocosa*, the best studied genus in relation to the behavioral significance of brushed front legs in males.

Diagnosis.—*Artoria schizocoides* is the



Figures 5–9.—*Artoria schizocoides*; male holotype (WAM T53800) and female paratype (WAMT53875), both from Bluff Knoll, Stirling Range National Park, Western Australia. 5. Left male pedipalp, ventral view; 6. Left male pedipalp, retrolateral view; 7. Left male pedipalp, apical part of bulb; 8. Epigynum, ventral view; 9. Epigynum, dorsal view. Scale bar: 5, 6 = 0.41 mm; 7 = 0.34 mm; 8, 9 = 0.55 mm.

only *Artoria* species known to the authors of which males have spatulate setae on the ventral side of the tibia of the first leg. The epigynum of females remotely resembles that of *A. cingulipes*, however, *A. schizocoides* is much smaller and darker in colorations.

Description.—*Male* (holotype WAM T53800): Carapace: dorsal line straight in lateral view, head flanks vertical; carapace very dark brown; brown median band, as wide as PLE anteriorly but narrowing and brightening posteriorly, distinctly yellow behind fovea; indistinct brown submarginal bands; head region very dark brown, base of eyes black; dark gray radial pattern; scarce cover of short white setae, slightly denser in head region; few longer bristles in head region; one very

long bristle between AME, two long bristles between ALE; AE strongly procurved. Sternum: yellow; gray pigmentation; sparsely covered with brown bristles, which are longer towards margins. Labium: brown, front end truncated and white. Chelicerae: dark brown, falces yellow; few long bristles in basal half; three retromarginal teeth, with the basal smallest, three promarginal teeth, with the medium largest. Pedipalp (Figs. 5–7, 10): cymbium dorsally with scopulate setae in apical half; apical tip of tegular apophysis bent ventrally, small protrusion on its apical edge; embolus reaches to about three quarters length of sclerotized groove of terminal apophysis (Fig. 7). Abdomen: dark olive gray; indistinct brown lanceolate heart mark in anterior half; mottled



Figure 10.—*Artoria schizocoides*; pedipalp of male from Alcoa mine site and forest, N and NW of Jarrahdale, Western Australia (WAM 97/584) in ventral view (SEM).

with brown spots; sparsely covered with white and, less dense, black setae; venter yellowish gray; three indistinct gray longitudinal bands; spinnerets with brown pigmentation. Legs: leg formula $IV > I > III > II$; femur I dark gray, femora II–IV dorsally brown with three indistinct dark annulations, ventrally yellow; tibia I black, ventrally with dense brush of spatulate setae (Fig. 4), tibiae II–IV light brown with indistinct annulations; metatarsus I yellow with contrasting black base, metatarsi II–IV brown with indistinct annulations; tarsus I yellow, tarsi II–IV brown; spination of leg I: Femur: 3 dorsal, 1 apicoprolateral; tibia: 3 ventral pairs, 2 prolateral; metatarsus: 3 ventral pairs; 1 apicoventral.

Female (based on paratype WAM T53875): Carapace and sternum: coloration and setae arrangement as male but carapace slightly

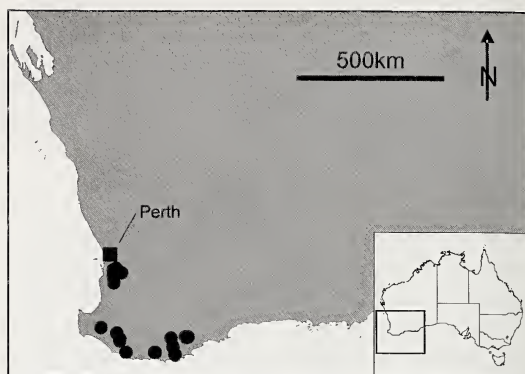


Figure 11.—Records of *Artoria schizocoides* in Western Australia.

lighter; AE strongly procurved. Labium: brown, front end truncated and white. Chelicerae: light brown, claws dark brown, brown bristles medially; dentition as male. Abdomen: dorsally uniformly olive-gray; indistinct lighter heartmark in anterior half and two light patches in posterior half; covered with short brown setae; venter olive-gray with irregular small yellow spots laterally and in two longitudinal lines medially; spinnerets yellow. Epigynum, ventral view (Fig. 8): Simple and round sclerotized ring, white centrally. Epigynum, dorsal view (Fig. 9): Large kidney-shaped complex of spermathecae and copulatory ducts. Legs: Leg formula $IV > II > I > III$; all segments light brown with distinct annulations; spination of leg I: Femur: 3 dorsal, 1 apicoprolateral; tibia: 2 ventral pairs, 1 apicoprolateral; metatarsus: 3 ventral pairs.

Measurements: male holotype WAM T53800 (female paratype WAM T53875): TL 3.24 (5.43), CL 1.88 (2.11), CW 1.30 (1.53). Eyes: AME 0.06 (0.06), ALE 0.06 (0.06), PME 0.26 (0.26), PLE 0.20 (0.20). Row of eyes: AE 0.35 (0.43), PME 0.69 (0.75), PLE 0.75 (0.87). Sternum (length/width) 0.87/0.81 (0.93/0.81). Labium (length/width) 0.23/0.20 (0.35/0.29). AL 1.56 (3.04), AW 0.98 (2.31). Legs: Lengths of segments (femur + patella/tibia + metatarsus + tarsus = total length): Pedipalp $0.69 + 0.61 + - + 0.66 = 1.96$, I $1.36 + 1.62 + 0.95 + 0.58 = 4.51$, II $1.27 + 1.45 + 0.95 + 0.58 = 4.25$, III $1.19 + 1.30 + 1.13 + 0.66 = 4.28$, IV $1.59 + 1.82 + 1.88 + 1.13 = 6.42$ (Pedipalp $0.67 + 0.75 + - + 0.52 = 1.94$, I $1.30 + 1.59 + 0.93 + 0.58 = 4.40$, II $1.27 + 1.50 + 1.01 + 0.55 = 4.33$,

III $1.24 + 1.45 + 1.16 + 0.61 = 4.46$, IV $1.53 + 2.11 + 1.88 + 0.81 = 6.33$).

Variation: males (females) (range, mean \pm s.d.): TL 3.32–3.90, 3.49 ± 0.22 ; CL 1.73–1.96, 1.79 ± 0.09 ; CW 1.21–1.39, 1.28 ± 0.05 ; $n = 10$ (TL 3.90–5.64, 4.64 ± 0.53 ; CL 1.79–2.17, 1.99 ± 0.17 ; CW 1.27–1.50, 1.36 ± 0.09 ; $n = 10$).

Distribution.—Southwest Western Australia (Fig. 11).

Natural history.—*Artoria schizocoides* appears to mature in winter. Most records of adult females and males are from a period between June and September, with occasional reports from October and November. The species seems to prefer dry to moderately moist forests in mountainous regions.

ACKNOWLEDGMENTS

We are indebted to Gail Stratton and Ansie Dippenaar-Schoeman who provided material for this study. Young-Bo Lee and An-Ja Ko (National Institute of Agricultural Science, Seoul, Korea) took the SEM photographs. Torbjörn Kronestedt provided helpful and constructive comments on an earlier draft of this manuscript. Julianne Waldoock initially directed the senior author's attention to the small brush-legged *A. schizocoides* in the collection of the WAM. This investigation forms part of a revision of Australian wolf spiders funded by the Australian Biological Resources Study (ABRS) to Mark Harvey (Western Australian Museum) and Andy Austin (University of Adelaide).

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Manuscript received 2 April 2006, revised 17 September 2006.

A NEW SPECIES OF *BRACHISTOSTERNUS* (SCORPIONES, BOTHRIURIDAE) FROM CHILE, WITH REMARKS ON *BRACHISTOSTERNUS CHILENSIS*

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ABSTRACT. *Brachistosternus* (*Leptosternus*) *aconcagua* new species, from the Chilean central Andes, is described. *Brachistosternus* (*L.*) *chilensis* Kraepelin 1911 is redescribed. Both species are related to other Andean species of the genus and with other species from central and northern Chile.

RESUMEN. Se describe a *Brachistosternus* (*Leptosternus*) *aconcagua* nueva especie de los Andes centrales Chilenos. Se redescribe a *Brachistosternus* (*L.*) *chilensis* Kraepelin 1911. Ambas especies se encuentran relacionadas con las especies andinas del género y con algunas especies del centro y norte de Chile.

Keywords: Taxonomy, morphology, Neotropics, South America, *Brachistosternus aconcagua*

The scorpion fauna of central Chile is still poorly known, with most of the published literature consisting of short species descriptions dating from the late 19th century and early 20th century (Pocock 1893, 1898; Kraepelin 1894, 1911; Lönnberg 1897; Mello-Leitão 1932; Werner 1939). Little subsequent taxonomic work on this fauna is available and the identity of most of the species from this area needs to be confirmed.

One of the most enigmatic Chilean species is *Brachistosternus* (*Leptosternus*) *chilensis* Kraepelin 1911. This species was briefly described by Kraepelin (1911) in a key, as a variety of *B. (L.) intermedius* Lönnberg 1902, based on a female specimen from La Ligua, Valparaíso Region, Chile. No illustrations and no data were provided about collectors, dates, depositories, or type material, and no other name-bearing specimen was previously designated. Since the original description, only a few authors mentioned this species again. Dr. E. Maury revised the scorpion collection of the Museo ed Instituto di Zoologia di Torino (MIZT) and found a scorpion from the type locality labeled: “*Br. intermedius chilensis* n. var. La Ligua; Aconcagua; Chile (Sc. 64),” and he supposed that this could be the specimen used by Kraepelin (1911) to prepare his

description (E. Maury, unpublished data). After that, he implicitly accepted the validity of *B. chilensis* as a valid species, listing it as a member of the subgenus *Leptosternus* (Maury 1973). We have been able to study this specimen at the MIZT, along with Maury’s notes, and we found a difference in the number of pectinal teeth with respect to the specimen described by Kraepelin (28–29 in the specimen from the MIZT, 30 in the specimen described by Kraepelin); so we can not be sure that this specimen was used by Kraepelin (1911) to describe the species. The original locality mentioned by Kraepelin is now highly altered by human activities and the surrounding region has been subjected to intense agricultural activities. Species of *Brachistosternus* are very sensitive to environmental changes, and after several collection trips to this place we only obtained specimens of *Bothriurus coriaceus* Pocock 1893 that is more resistant to environmental changes. However, in nearby localities around La Ligua with better preserved environments, we were only able to collect a single species of *Brachistosternus*. This species is very common throughout this area and its external morphology matches the few characteristics described by Kraepelin (1911) in his description of *B. chilensis*, and corre-

sponds to the characteristics of the specimen deposited at the MIZT. Therefore, to maintain stability we consider this species as *B. chilensis*, which is redescribed in this paper.

While revising material from central Chile we have also recognized an undescribed species of *Brachistosternus* that is herein described. This species is very similar to *B. chilensis* but inhabits a slightly different environment at intermediate altitudes of the western central Andes. Both species described in this paper are similar to the Andean species of the genus as well as to other species from central and northern Chile.

METHODS

The terminology used for the hemispermatophore structures follows Maury (1974). Trichobothrial terminology follows Vachon (1974). Terminology of the androvestigia follows Cekalovic (1973). Terminology of the telson gland follows Roig Alsina & Maury (1981). Terminology of the metasomal carinae follows Stahnke (1970), abbreviated as follows: DL = dorsal lateral; LSM = lateral supramedian; LIM = lateral inframedian; VL = ventral lateral; VM = ventral median. Specimens from the following institutions were examined: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," National Arachnological Collection, Argentina (MACN-Ar); Museo ed Instituto di Zoologia, Torino, Italia (MIZT); American Museum of Natural History, New York, USA (AMNH); Cátedra de Diversidad Animal I, Universidad de Córdoba, Córdoba, Argentina (CDA); Museo Zoológico del Instituto de Biología de la Universidad de Concepción, Concepción, Chile (MZUC). All measurements are given in mm, and were taken using an ocular micrometer. Illustrations were produced using a stereomicroscope and camera lucida. The hemispermatophores were dissected from surrounding tissues and observed in 80% ethanol. Localities of *Brachistosternus* (*Leptosternus*) *negrei* Cekalovic 1975 depicted in Fig. 27 were taken from Ojanguren-Affilastro (2005).

TAXONOMY

Family Bothriuridae Simon 1880

Genus *Brachistosternus* Pocock 1893

Type species.—*Scorpio ehrenbergii* Ger-
vais 1841, by original designation.

Subgenus *Brachistosternus*
(*Leptosternus*) Maury 1973

Type species.—*Telegonus weijenberghii*
Thorell 1876, by original designation.

Brachistosternus (*Leptosternus*)

aconcagua new species

Figs. 1–13, 27

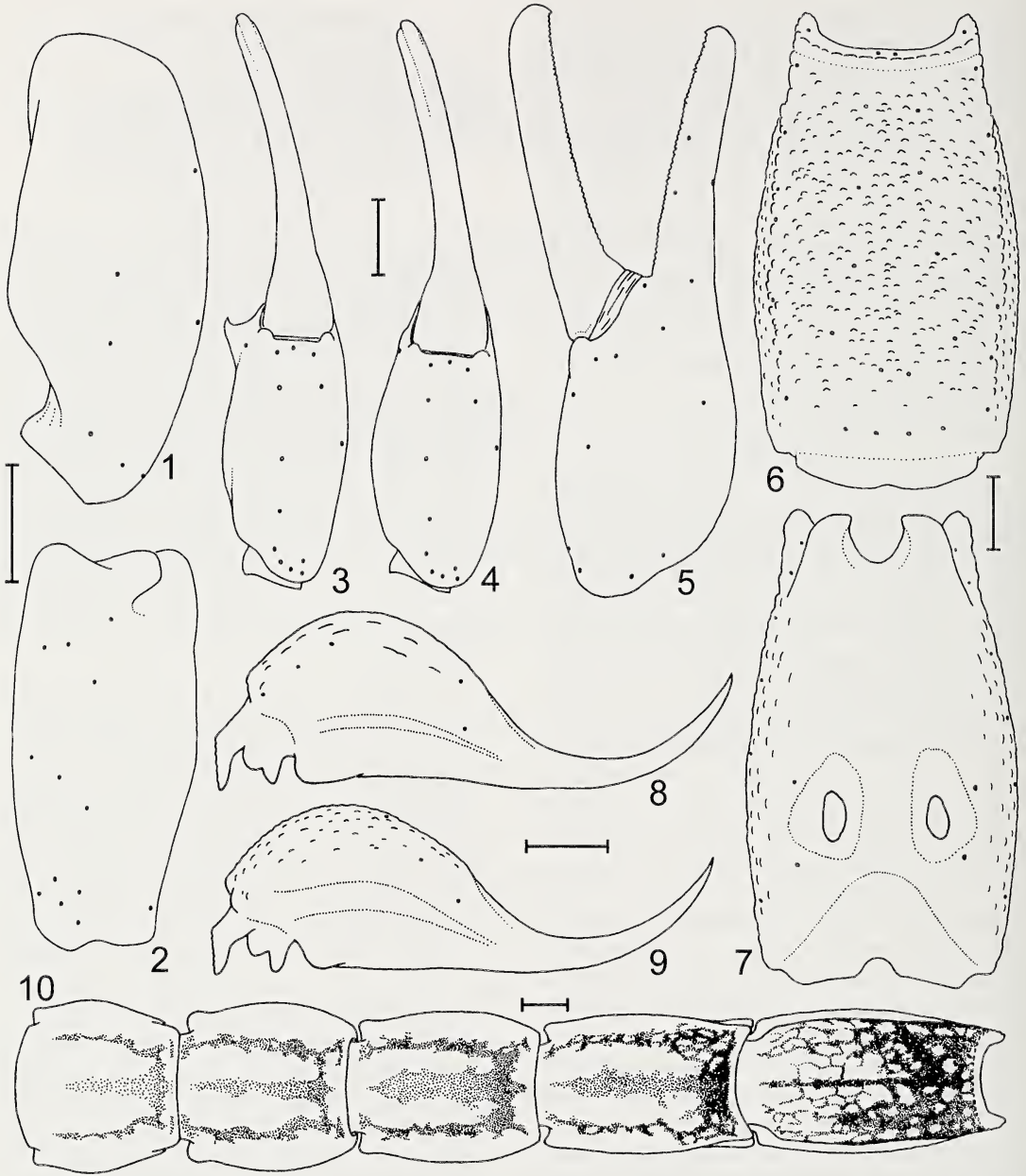
Material examined.—Holotype male, CHILE, *Valparaíso*, between Río Blanco and Juncal, 32°54'00"S, 70°11'00"W, 1950 m a.s.l., 6 January 1984, Roig Alsina (MACN-Ar 10767). Paratypes: CHILE: *Valparaíso*: 1 female, 1 juvenile, Guardia Vieja, 32°53'60"S, 70°16'60"W, 1600 m, 19 January 1984, E. Maury (MACN-Ar 10768); 3 females, 3 juveniles, Juncal, 32°52'00"S, 70°10'00"W, 1950 m, 5 January 1984, E. Maury (MACN-Ar 10769); 1 juvenile, 20 km from Portezuelo, 32°53'00"S, 70°13'00"W, 2100 m, 13 February 2005, Ojanguren & Korob (MACN-Ar 10770).

Etymology.—The specific name is a noun in apposition referring to the Aconcagua mountain, the highest peak of America, situated very close to the type locality.

Diagnosis.—*Brachistosternus aconcagua* is most similar to *B. chilensis*, and both species can be distinguished by the pigmentation pattern of the ventral surface of the metasoma: in *B. aconcagua* the VM stripe of segments I–IV is thick, faint, and joins distally with the LV stripes (Fig. 10), whereas in *B. chilensis* the VM stripe is very thin and well marked, and never joins with the LV stripes (Fig. 25). Other morphological differences between these species include: the metasomal glands or androvestigia of *B. aconcagua* are very small (Fig. 7) whereas in *B. chilensis* they are of medium size (Fig. 22); in *B. chilensis* the VM carinae of metasomal segment V extends almost the entire length of the segment, but is poorly developed (Fig. 21), whereas in *B. aconcagua* it is absent (Fig. 6).

Brachistosternus (*L.*) *aconcagua* is also similar to *B. negrei*. Both species can be easily distinguished because in *B. negrei* the VM stripe of metasomal segments I–IV is divided into 2 thin PM stripes (Fig. 26).

Description.—**Color:** general color dark yellow, with very dense dusky pattern. Carapace with front edge densely pigmented; ocular tubercle black, with a dark stripe from



Figures 1-10.—*Brachistosternus (Leptosternus) aconcagua* new species: 1. Left pedipalp patella, ventral aspect; 2. Left pedipalp patella, external aspect; 3. Left pedipalp chela, male, ventral aspect; 4. Left pedipalp chela, female, ventral aspect; 5. Left pedipalp chela, female, external aspect; 6. Fifth metasomal segment, male, ventral aspect; 7. Fifth metasomal segment, male, dorsal aspect; 8. Telson, female, lateral aspect; 9. Telson, male, lateral aspect; 10. Metasoma, pigmentation pattern, ventral aspect. Scale bars = 1 mm.

postocular furrow to lateral ocelli, leaving an anterior depigmented triangle that only in very pigmented specimens is pigmented; lateral surface with dark reticulated pigment; with 2 posterolateral dark spots. Tergites with

2 well developed lateral dark spots that leave an incomplete depigmented stripe between them; these lateral spots are joined only by a thin dark line on the posterior margin of segment. Pedipalps: femur and patella densely

Table 1.—Measurements (mm) of *Brachistosternus aconcagua* new species, male holotype (MACN-Ar 10767), and female paratype (MACN-Ar 10768), and *Brachistosternus chilensis*, male (MACN-Ar 10772) and female (MACN-Ar 10773).

	<i>Brachistosternus</i> (L.) <i>aconcagua</i>		<i>Brachistosternus</i> (L.) <i>chilensis</i>	
	Male holotype	Female paratype	Male	Female
Total length	43.20	57.12	49.33	53.36
Carapace, length	5.09	6.38	5.41	6.87
Carapace, anterior width	3.86	5.01	4.28	5.09
Carapace, posterior width	5.66	7.11	6.06	7.03
Mesosoma, total length	11.08	18.74	15.00	13.86
Metasoma, total length	27.03	32.00	22.62	25.12
Metasomal segment I, length	3.20	4.36	3.64	4.04
Metasomal segment I, width	3.80	4.68	4.12	4.68
Metasomal segment I, height	2.91	3.63	3.07	3.47
Metasomal segment II, length	3.80	4.85	4.04	4.52
Metasomal segment II, width	3.47	4.20	3.79	4.28
Metasomal segment II, height	2.91	3.72	3.07	3.47
Metasomal segment III, length	4.00	4.85	4.20	4.85
Metasomal segment III, width	3.23	4.04	3.64	4.12
Metasomal segment III, height	2.91	3.47	2.99	3.47
Metasomal segment IV, length	4.72	5.25	4.85	5.49
Metasomal segment IV, width	3.15	3.79	3.31	3.88
Metasomal segment IV, height	2.83	3.23	2.91	3.23
Metasomal segment V, length	5.25	6.06	5.89	6.22
Metasomal segment V, width	3.31	3.64	3.31	3.88
Metasomal segment V, height	2.67	2.99	2.5	2.91
Telson, length	6.06	6.63	6.3	7.51
Vesicle, length	3.55	3.63	3.23	3.88
Vesicle, width	2.18	2.50	2.18	2.58
Vesicle, height	2.02	2.18	1.86	2.34
Aculeus, length	2.51	2.99	3.07	3.63
Femur, length	4.36	4.44	3.88	4.28
Femur, width	1.21	1.21	1.05	1.45
Patella, length	4.04	4.44	3.88	4.12
Patella, width	1.54	1.94	1.54	1.78
Chela, length	7.27	7.99	6.86	7.67
Chela, width	1.61	1.94	1.77	1.94
Chela, height	2.18	2.42	2.26	2.66
Movable finger, length	4.28	4.68	4.12	4.36

pigmented, chela with longitudinal dark stripes on hand, and with a dark spot on base of movable finger, fingers depigmented. Legs: femur and patella densely pigmented. Metasoma: segments I–III: dorsally with median thin spot and 2 posterolateral dark spots, laterally with reticulate pigment near dorsal margin, ventrally with 2 lateral thin dark stripes, and median thick stripe faintly marked, these 3 stripes join on posterior third of segment (Fig. 10); segment IV similar to segments I–III but median ventral dark stripe is well marked; segment V: dorsal surface with 2 posterolateral dark spots poorly marked, lateral

surface like segments I–IV, ventral surface with 2 wide dark stripes and thin median stripe, connected in anterior half of segment by dense reticulated pigmentation, and join in posterior half of segment. Telson: vesicle faintly spotted on ventral surface, aculeus densely pigmented.

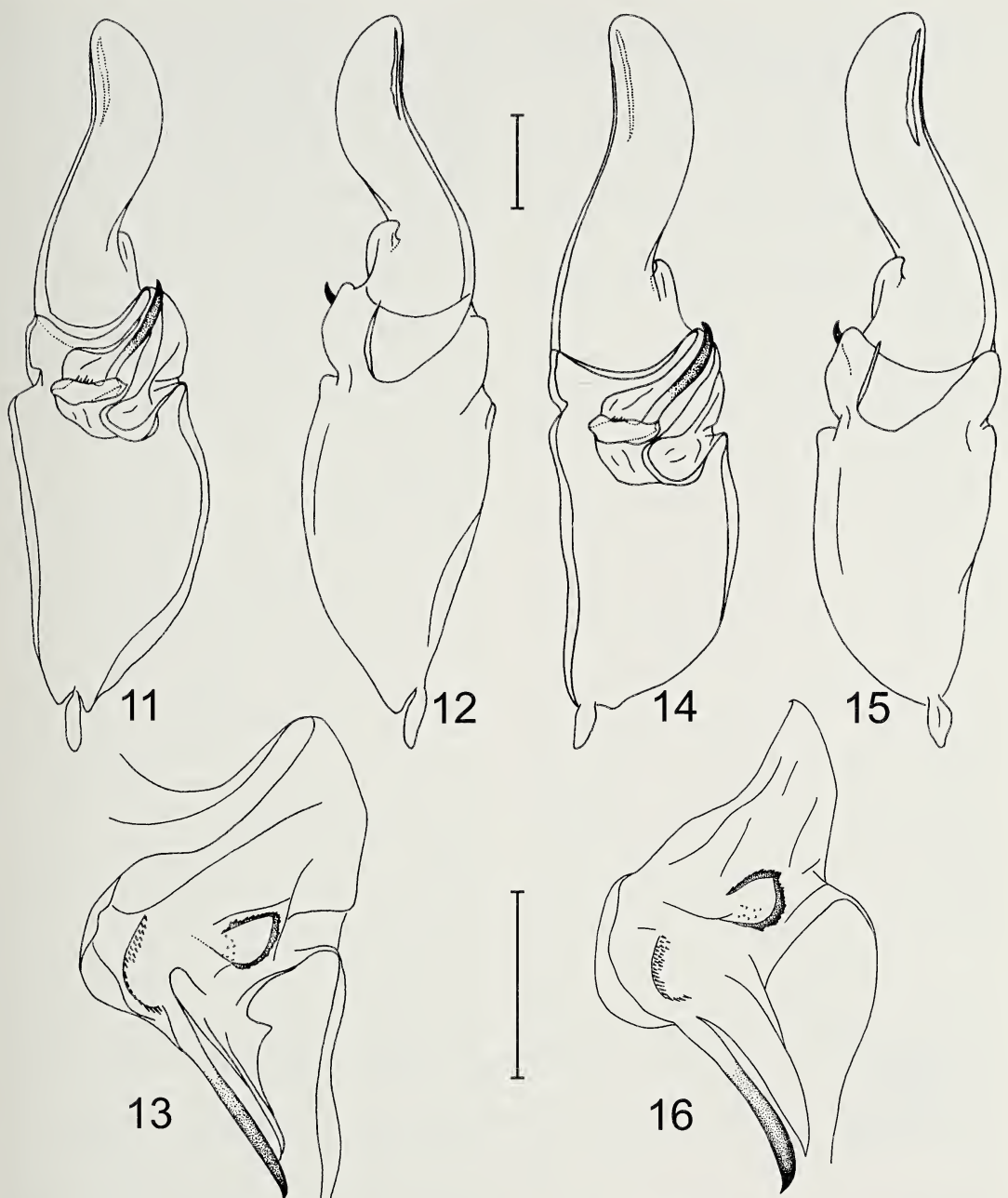
Morphology: measurements of male holotype, and female paratype in Table 1. Chelicerae with 2 subdistal teeth. Carapace: anterior margin with a well developed median bulge; anterior longitudinal sulcus deeply marked; tegument densely granulate in male holotype, smooth in females; ocular tubercle well

marked, slightly anterior to middle of carapace, interocular sulcus deeply marked, eyes 2 diameters apart, lateral sulcus, postocular furrow, and posterior sulcus deeply marked. Sternum: sternum type 2 (Soleglad & Fet 2003) much wider than long, apex width almost equal to posterior width, posterior emargination well developed, with convex lateral lobes conspicuously separated. Tergites I–VI with smooth tegument in anterior two-thirds, and slightly granulate in posterior third; tergite VII with granulate tegument and 2 posterolateral keels. Sternites: very granulate in males, smooth in females; spiracles long and narrow, placed in very conspicuous furrow. Metasoma: segments I–III: dorsal surface very granulate in male holotype, smooth in females, DL carinae extend entire length of segment but poorly developed; lateral surface granulate in male holotype, smooth in females, LIM and LSM carinae poorly developed, extending entire length of segment in male holotype, but only in posterior half of segment in females; ventral surface granulate in male holotype, smooth in females; segment IV: ventral surface smooth and covered by scattered setae, LIM and LSM carinae absent, others similar to segments I–III; segment V: dorsal and lateral surfaces granulate in male holotype, smooth in females, androvestigia poorly developed and occupy less than 20 % of dorsal surface of segment (Fig. 7), ventral surface densely granulate (Fig. 6); ventral setae usually comprising 5 or 6 rows, the first 2 rows with 4 or 5 setae, remainder with 1–3 setae; VL carinae well marked, extending entire length of segment, VM carina absent. Telson: vesicle with rounded ventral surface, tegument sparsely granulate; no evident telson gland in male; aculeus slightly curved, same length as vesicle (Figs. 8, 9). Pedipalps: trichobothrial pattern of subgenus *Leptosternus*, neobothriotaxic major type C (Figs. 1–5), adding 1 trichobothria on ventral series of chela; femur with 3 trichobothria: 1 *d*, 1 *i* and 1 *e*; patella with 19 trichobothria (Figs. 1, 2): 3 *V*, 2 *d*, 1 *i*, 3 *et*, 1 *est*, 2 *em*, 2 *esb*, and 5 *eb*; chela with 27 trichobothria (Figs. 3–5): 1 *Est*, 5 *Et*, 5 *V*, 1 *Esb*, 3 *Eb*, 1 *Dt*, 1 *Db*, 1 *et*, 1 *est*, 1 *esb*, 1 *eb*, 1 *dt*, 1 *dst*, 1 *dsb*, 1 *db*, 1 *ib*, 1 *it*; femur with DI, DE and VI carinae well marked, remainder of tegument smooth; patella: DI and VI carinae well marked in male holotype, absent in females, remainder of teg-

ument smooth; chela: narrow, with smooth tegument and VM carina well developed; fingers with a median row of teeth and 7–9 pairs of additional teeth, internal apophysis of male very well developed (Fig. 3). Legs: femur and patella with finely granulate tegument, and poorly developed carinae on ventral surface; telotarsal unguis approximately of same size on all legs. Hemispermaphore: distal lamina thick, slightly curved, almost of same size as basal portion (Figs. 11, 12); cylindrical apophysis well developed, longer than laminar apophysis; basal triangle well developed, formed by 3 crests; internal spines absent, basal spines and row of spines well developed and on same line (Fig. 13).

Variability.—Pedipalp chela length/height ratio, 3.3 (♂ holotype); 3.2–3.33 (♀, *n* = 4; mean = 3.28). Pedipalp chela length/width ratio: 4.3 (♂ holotype); 4.28–4.36 (♀, *n* = 4; mean = 4.31). Metasomal segment V length/width ratio, 1.56 (♂ holotype); 1.50–1.73 (♀, *n* = 4; mean = 1.61). Metasomal segment V, ventral setae: 13–15 (*n* = 10; median = 14). Metasomal segment V, lateroventral setae: 8–9 (*n* = 10; median = 8). Telotarsus III dorsal setae: 9–11 (*n* = 10; median = 11). Telotarsus I dorsal setae: 7–8 (*n* = 10; median = 7). Telotarsus I ventrointernal setae: 2–3 (*n* = 10; median = 2). Telotarsus I ventroexternal setae: 0 (*n* = 5; median = 0). Basitarsus I dorsal setae: 5–6 (*n* = 10; median = 6). Telotarsus II dorsal setae: 8–9 (*n* = 10; median = 9). Telotarsus II ventrointernal setae: 3–4 (*n* = 10; median = 4). Telotarsus II ventroexternal setae: 2–3 (*n* = 10; median = 3). Basitarsus II dorsal setae: 6–7 (*n* = 10; median = 6). Telotarsus III ventrointernal setae: 6–7 (*n* = 10; median = 6). Telotarsus III ventroexternal setae: 3–5 (*n* = 10; median = 3). Basitarsus III dorsal setae: 5–6 (*n* = 10; median = 6). Telotarsus IV dorsal setae: 4–5 (*n* = 10; median = 5). Telotarsus IV ventrointernal setae: 4–5 (*n* = 10; median = 5). Telotarsus IV ventroexternal setae: 3–5 (*n* = 10; median = 4). Basitarsus IV dorsal setae: 3–4 (*n* = 10; median = 3). Pectinal teeth: 34 and 36 (♂, *n* = 2), 28–31 (♀, *n* = 8; median = 31). Total length (mm): 43.2 (♂ holotype); 50.4–61.0 (♀, *n* = 4; median = 55.25).

Distribution.—*Brachistosternus aconagua* has been collected within a small area of central Chile, in the Valparaíso Region (Fig. 27). All specimens were collected on the



Figures 11–16.—11–13. *Brachistosternus (Leptosternus) aconcagua* new species: 11. Left hemispermatophore, ventral aspect; 12. Left hemispermatophore, dorsal aspect; 13. Left hemispermatophore, detail of the lobe region. 14–16. *Brachistosternus (Leptosternus) chilensis* Kraepelin: 14. Left hemispermatophore, ventral aspect; 15. Left hemispermatophore, dorsal aspect; 16. Left hemispermatophore, detail of the lobe region Scale bars = 1 mm.

western slopes of west Andes, at intermediate altitudes between 1600 and 2100 m a.s.l.; all these localities belong to the “Andes Mediterraneos” botanical subregion, placed in the

“Estepa altoandina” botanical region (Gajardo 1993).
Ecology.—*Brachistosternus aconcagua* has been collected in sympatry with *B. coriaceus*.

Brachistosternus (Leptosternus) chilensis
Kraepelin 1911
Figs. 14–25, 27

Brachistosternus intermedius chilensis Kraepelin 1911:87.

Brachistosternus (Leptosternus) chilensis: Maury 1973:249; Cekalovic 1983:55; Masnú de Moreno 1991:185.

Brachistosternus chilensis: Kovařík 1998:100; Lowe & Fet 2000:49, 50; Ojanguren Affilastro 2005:191.

Type material.—Kraepelin (1911) did not designate any specimen as type material, but he based his description on at least one female specimen from La Ligua, 32°26'S, 71°14'W, Valparaíso Region, Chile.

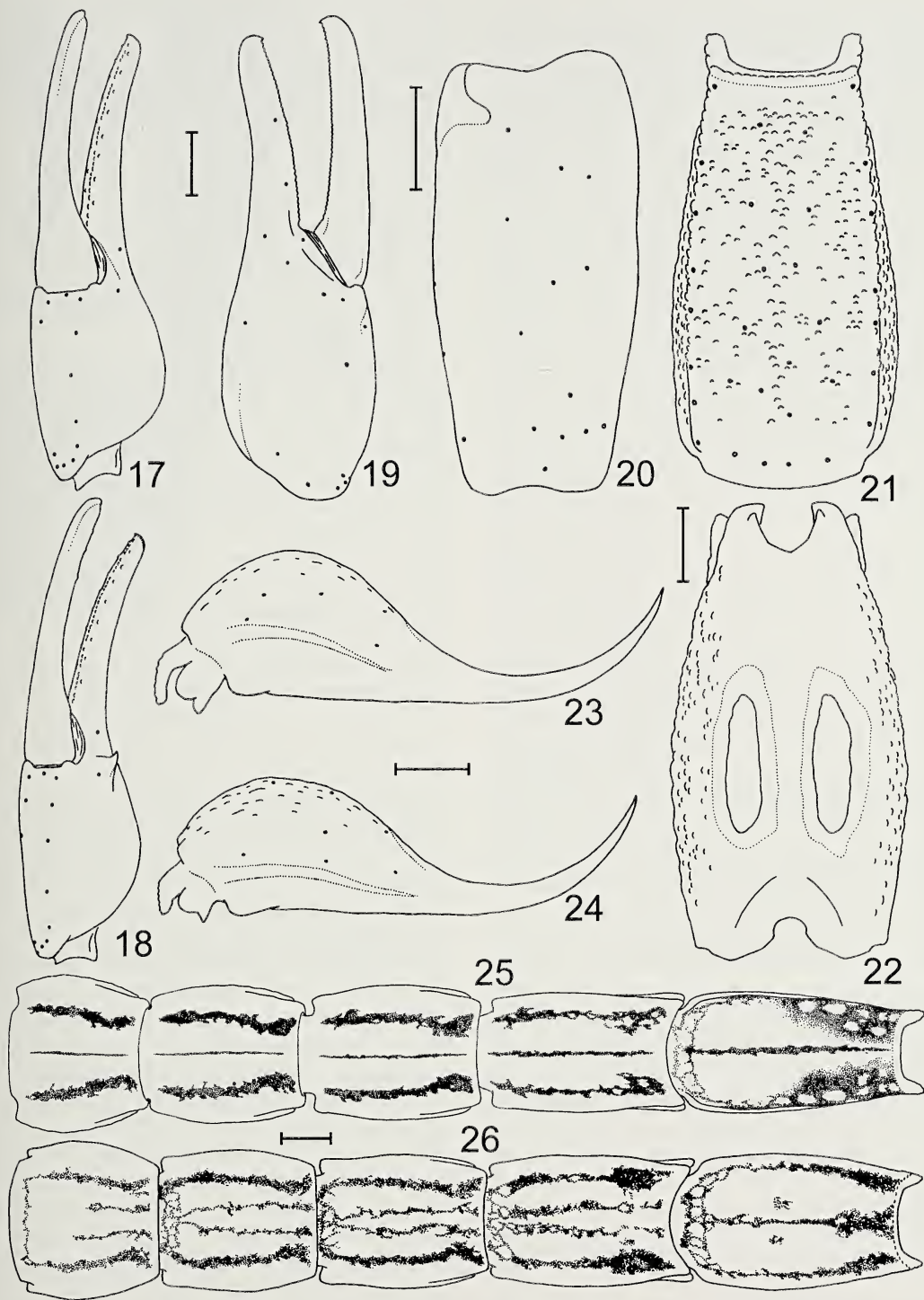
Material examined.—CHILE: *Region V Valparaíso*: 1 ♂, “La Campana” National Park, Palmas de Ocoa Sector, 500 m a.s.l., 32°56'33.4"S, 71°05'02.1"W, 14 February 2005, Korob & Ojanguren Affilastro (MACN-Ar 10772); 2 ♀, 2 juveniles, same data (MACN-Ar 10773); 2 ♀, 2 juveniles, 1 ♂, same data (MZUC); 3 ♂, 2 ♀, 1 juvenile, same locality, 12 November 2003, Ochoa, Mattoni & Prendini (CDA); 1 ♀, La Ligua, 32°26'S, 71°14'W (MIZT); 1 ♂, Villa Alemana, 33°03'S, 71°22'W, February 1968, Cruzat (MACN-Ar 10774); 1 ♂, Quinteros, 32°47'S, 71°32'W, January 1983, Passera (MACN-Ar 10775); 1 ♂, Santiago-Valparaíso, 33°02'S, 71°27'W, April 1970, Fritz (MACN-Ar 10776); *Región Metropolitana de Santiago*: 2 ♀, 1 juvenile, Baños de Morales, 33°49'S, 70°12'W, 29 January 1968, Mesa (MACN-Ar 10777); 1 ♂, Cajón del Maipo, Río Colorado, 33°36'S, 70°22'W, 29 February 1986, Peña (MACN-Ar 10778); 1 juvenile, El Manzano, 34°06'S, 71°51'W, August 1970, Jackson (AMNH); 1 ♀, El Arbol, Aculeo, 33°52'S, 70°55'W, October 1979, Peña (AMNH).

Diagnosis.—This species is similar to *B. aconcagua*, and each can be distinguished by the pigmentation pattern of the ventral surface of the metasoma; in *B. aconcagua* the VM stripe of segments I–IV is thick, faint, and joins distally with the LV stripes (Fig. 10), whereas in *B. chilensis* the VM stripe is very thin and well marked, and never joins with the LV stripes (Fig. 25). Other morphological differences between these species include: metasomal glands or androvestigia of *B. acon-*

cagua are very small (Fig. 7), whereas in *B. chilensis* they are of medium size (Fig. 22); in *B. chilensis* the VM carinae of metasomal segment V extends almost the entire length of the segment, but is poorly developed (Fig. 21), whereas in *B. aconcagua* it is absent (Fig. 6). It is also similar to *B. negrei*, and each species can be easily distinguished because in *B. negrei* the VM stripe of metasomal segments I–IV is divided in 2 thin PM stripes (Fig. 26), whereas in *B. chilensis* there is only a thin VM dark stripe (Fig. 25). *Brachistosternus chilensis* also has more developed androvestigia, occupying approximately 50% of the dorsal surface of metasomal segment V whereas in *B. negrei* they occupy 20–30% of the dorsal surface.

Description.—*Color*: general color dark yellow with dense dusky pattern. Chelicerae: depigmented. Carapace: with 2 thick dark stripes from postocular furrow to lateral ocelli leaving a depigmented triangle on front margin; ocular tubercle and area around lateral ocelli black; posterior margin with 2 posterolateral dark spots, remainder depigmented. Pedipalps: femur and patella densely pigmented; chela almost completely depigmented, with longitudinal faint dark stripes on hand, fingers depigmented. Legs: femur and patella with light reticular pigment near articulation, remainder depigmented. Tergites I–VI with 2 lateral dark spots and 2 PM dark spots, in some specimens PM spots can join forming a median spot; in very pigmented specimens the 4 spots are connected by reticular pigment; tergite VII: with 2 posterolateral dark spots. Sternites: depigmented. Metasoma: segments I–III dorsally with a thin median spot near anterior margin, and 2 posterolateral spots; lateral surface depigmented; ventral surface with a VM and 2 thin LV dark stripes that do not join (Fig. 25); segment IV: similar to segments I–III but with posterolateral dorsal dark spots faintly marked; segment V: dorsal and lateral surfaces depigmented; ventral surface with VM thin dark stripe and 2 LV thick stripes that in most specimens do not join, only in most pigmented specimens they join in posterior margin of segment. Telson: vesicle faintly pigmented on ventral surface; aculeus dark brown.

Morphology: measurements of a male (MACN-Ar 10772) and a female (MACN-Ar 10773) specimen in Table 1. Chelicerae: with



Figures 17–26.—17–25. *Brachistosternus (Leptosternus) chilensis* Kraepelin: 17. Right pedipalp chela, female, ventral aspect; 18. Right pedipalp chela, male, ventral aspect; 19. Right pedipalp chela, female, external aspect; 20. Right pedipalp patella, external aspect; 21. Fifth metasomal segment, male, ventral aspect; 22. Fifth metasomal segment, male, dorsal aspect; 23. Telson, female, lateral aspect; 24. Telson, male, lateral aspect; 25. Metasoma, pigmentation pattern, ventral aspect. 26. *Brachistosternus (Leptosternus) negrei* Cekalovic: Metasoma, pigmentation pattern, ventral aspect. Scale bars = 1 mm.

2 small subdistal teeth. Carapace: anterior margin with slight median bulge; tegument slightly granulate in females, densely granulate in males; anterior longitudinal sulcus deeply marked; ocular tubercle well defined in middle of carapace, interocular sulcus deeply incised, median eyes 2 diameters apart; lateral sulcus, postocular furrow and posterior sulcus deeply incised. Sternum: sternum type 2 (Soleglad & Fet 2003) much wider than long, apex width slightly narrower than posterior width, posterior emargination quite well developed, with convex lateral lobes conspicuously separated. Tergites I–VI with smooth tegument, except near posterior margin where it is slightly granulate; tergite VII: with scattered granulation and 2 posterolateral keels. Sternites with densely granulate tegument; spiracles long and narrow. Metasoma: segment I: dorsal surface granulate; lateral surface granulate, DL, LSM and LIM carinae only present in posterior two-thirds of segment; ventral surface very granulate; segments II and III similar to segment I but less granulate, and with carinae present only in second half of segment; segment IV: dorsal surface smooth; lateral surface granulate; ventral surface with scattered setae, slightly granulate in males, smooth in females; segment V: dorsal surface smooth; in males, androvestigia are of medium size (Fig. 22); lateral surface granulate; ventral surface densely granulate (Fig. 21), VM and LV carinae almost complete, with 4–6 rows of ventral setae, first 2 rows of 4–6 setae, remainder of 1 or 2 setae. Telson: vesicle small, ventral surface slightly granulate (Figs. 23, 24); in males there is no evident telson gland on the dorsal surface; aculeus slightly curved, and slightly longer than vesicle. Pedipalps: trichobothrial pattern typical of subgenus *Leptosternus*, neobothriotaxic major type C, adding 1 trichobothria on ventral series of chela; femur with 3 trichobothria: 1 *d*, 1 *i* and 1 *e*; patella with 19 trichobothria (Fig. 20): 3 *V*, 2 *d*, 1 *i*, 3 *et*, 1 *est*, 2 *em*, 2 *esb*, and 5 *eb*; chela with 27 trichobothria (Figs. 17–19): 1 *Est*, 5 *Et*, 5 *V*, 1 *Esb*, 3 *Eb*, 1 *Dt*, 1 *Db*, 1 *et*, 1 *est*, 1 *esb*, 1 *eb*, 1 *dt*, 1 *dst*, 1 *dsb*, 1 *db*, 1 *ib*, 1 *ir*; femur with DI, DE and VI carinae well marked, remainder of tegument smooth, patella: DI and VI carinae well marked in male holotype, absent in females, remainder of tegument smooth; chela: narrow, with smooth tegument and VM

carina well developed; fingers with a median row of teeth and 7–9 pairs of additional teeth, internal apophysis of male very well developed (Fig. 18). Legs: tegument smooth; telotarsal unguis of the same size. Hemispermatophore: distal lamina thick, slightly curved, of same size or slightly shorter than basal portion (Fig. 15); cylindrical apophysis well developed, longer than laminar apophysis (Fig. 14); basal triangle well developed, formed by 2 or 3 crests; internal spines absent, basal spines and row of spines well developed and on same line (Fig. 16).

Variability.—Pedipalp chela length/height ratio, 3.15–3.37 (δ , $n = 8$; mean = 3.26); 2.87–3.2 (φ , $n = 8$; mean = 3.02). Pedipalp chela length/width ratio, 4.06–4.4 (δ , $n = 8$; mean = 4.28); 3.81–4.17 (φ , $n = 8$; mean = 4.02). Metasomal segment V, length/width ratio, 1.66–1.74 (δ , $n = 8$; mean = 1.68); 1.56–1.66 (φ , $n = 8$; mean = 1.59). Metasomal segment V, ventral setae: 12–17 ($n = 10$; median = 14). Metasomal segment V, lateroventral setae: 8–10 ($n = 12$; median = 9). Telotarsus I dorsal setae: 7–9 ($n = 10$; median = 8). Telotarsus I ventrointernal setae: 1–3 ($n = 10$; median = 3). Telotarsus I ventroexternal setae: 0 ($n = 10$; median = 0). Basitarsus I dorsal setae: 6–7 ($n = 10$; median = 6). Telotarsus II dorsal setae: 8–10 ($n = 10$; median = 8). Telotarsus II ventrointernal setae: 3–5 ($n = 10$; median = 4). Telotarsus II ventroexternal setae: 2–3 ($n = 10$; median = 2). Basitarsus II dorsal setae: 6–7 ($n = 10$; median = 7). Telotarsus III, dorsal setae: 8–11 ($n = 10$; median = 10). Telotarsus III, ventrointernal setae: 5–8 ($n = 12$; median = 6). Telotarsus III, ventroexternal setae: 4–6 ($n = 12$; median = 5). Basitarsus III, dorsal setae: 6–8 ($n = 12$; median = 6). Telotarsus IV dorsal setae: 4–5 ($n = 10$; median = 4). Telotarsus IV ventrointernal setae: 3–5 ($n = 10$; median = 5). Telotarsus IV ventroexternal setae: 2–5 ($n = 10$; median = 5). Basitarsus IV dorsal setae: 3–4 ($n = 10$; median = 3). Pectinal teeth: 28–34 (δ , $n = 8$; median = 33), 28–34 (φ , $n = 9$; median = 30). Total length (mm): 43–59 (δ , $n = 9$; median = 49.6); 48–56 ($n = 10$; median = 51.5).

Distribution.—*Brachistosternus chilensis* occurs in Region V Valparaíso and in Region Metropolitana, de Santiago, Chile, from sea level to 1000 m a.s.l. (Fig. 27); all of the localities where this species has been collected



Figure 27.—Map showing known distribution records of *Brachistosternus* (*Leptosternus*) *aconcagua* new species, *B. (L.) chilensis* Kraepelin, and *B. (L.) negrei* Cekalovic.

belong to the “Bosque Esclerófilo” botanical subregion, placed in the “Matorral y Bosque Xerófilo” botanical region (Gajardo 1993). Some of the specimens collected at “Region Metropolitana de Santiago,” are subtly different from the specimens from Valparaíso, but we have decided to consider these differences as intraspecific variation.

Ecology.—*Brachistosternus chilensis* has been collected in sympatry with *B. coriaceus* and *Caraboctonus keyserlingi* Pocock 1893.

ACKNOWLEDGMENTS

We are especially grateful to Arturo Roig Alsina who has donated the type specimen of *B. aconcagua* to the MACN-AR. We are grateful to Ivan Benoit of “Corporacion Nacional Forestal” (CONAF) who has been very helpful with the authorizations of Chilean National Parks; to Lorenzo Prendini and Camilo Mattoni, for the loan of specimens and for allowing access to AMNH and CDA scorpion collections; to Lisa Levi for allowing access to the MIZT scorpion collection; to Paula Korob for her assistance on collecting trips. We are

grateful to Lorenzo Prendini, Victor Fet, Mark Harvey and Paula Cushing for their helpful comments on the manuscript. This research was partially supported by a postgraduate grant from the “Consejo Nacional de Investigaciones Científicas y Técnicas” (CONICET) to Andrés Ojanguren.

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Manuscript received 8 March 2006, revised 9 August 2006.

SPIDERS OF THE GENUS *DRACONARIUS* (ARANEAE, AMAUROBIIDAE) FROM KOREA

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ABSTRACT. Three species of the genus *Draconarius* are recognized from Korea and all are described and illustrated. *Coelotes kayasanensis* Paik 1972 is transferred to *Draconarius* (*D. kayasanensis* new combination) based on the presence of a patellar apophysis, the hooked dorsal apophysis of the conductor in the male palp, the position of the spermathecal head, and the shape of the broadly rectangular genital opening of the female situated posteriorly near the epigastric furrow. The male of *D. coreanus* (Paik & Yaginuma 1969) and the female of *D. kayasanensis* are described for the first time. A neotype of *D. coreanus* is designated in the present study because of the loss of the holotype, limited range of the species, and the small population size. *Draconarius hallaensis* new species is described and is distinguished by its small size (less than 8 mm in total body length), large rounded retrolateral tibial apophysis, and median apophysis that has a distally divided thumb-shaped inner part.

Keywords: Taxonomy, spiders, Coelotinae, Asia, morphology

The Holarctic spider subfamily Coelotinae is one of the most common spider taxa in the region and is comprised of at least 373 species (Wang 2002, 2003, 2006; Platnick 2006). Wang (2002) revised the subfamily Coelotinae at the generic level based on 31 characters and 22 taxa, including two outgroup taxa (*Tamgrinia* Lehtinen 1967 and *Amaurobius* C.L. Koch 1837). Of these, the genus *Draconarius* Ovtchinnikov 1999 includes a total of 95 species from a variety of Asian countries (China, 77 species; Thailand, 10; Bhutan, 4; Nepal, 1; Tajikistan, 1; Taiwan, 1; Korea, 1). These taxa are characterized by posteriorly originating copulatory ducts, the presence of a dorsal apophysis on the conductor, and the cymbial furrow more than half the cymbial length. More than 60 species of *Draconarius* are described only from male or female specimens and the genus has been previously included in *Coelotes* Blackwall 1841 (Zhang et al. 2002; Dankittipakul & Wang 2003, 2004; Dankittipakul et al. 2005). This paper revises the species of *Draconarius* found in Korea.

The only species of *Draconarius* currently recorded from Korea, originally named as *Coelotes coreanus* Paik & Yaginuma 1969, was described from a female specimen taken in Seong lava cave, Jeju-do Island, Korea (Paik et al. 1969). Although Namkung (2002,

2003) presented simple illustrations of *D. coreanus*, the species cannot be reliably identified from his pictorial book. Wang (2003) reported *D. coreanus* from two different localities (a female from Mt. Kwanak, Seoul and a male from Mt. Halla, Jeju-do Island). However, his description seemed to be based on misidentified specimens. In this paper, we describe *D. hallaensis* new species based on specimens formerly known as *D. coreanus* collected from Mt. Halla and the additional samples from the Korean National Arboretum of Gwangreung, Gyeonggi-do, in western central Korea.

The holotype of *D. coreanus* has either been lost within the collection of the National Science Museum in Tokyo, Japan, or an error was made by the original authors preventing its correct identification. The type locality of *D. coreanus* (Seong lava cave) was surveyed ten times between August 2003 and January 2006 and we found several specimens which are described here. A neotype for this species is designated from these samples and redescribed, along with the first description of males.

Draconarius kayasanensis Paik 1972 was first named as *Coelotes kayasanensis*, and based only on a single male (Paik 1972). However, Ovtchinnikov (1999) and Wang

(2002) transferred the species to *Ambanus* Ovtchinnikov 1999 without detailed examination. We collected many specimens of *D. kayasanensis* using pitfall traps and active searching in Mt. Odae National Park in eastern Korea, approximately 100 km from Seoul. After a careful reexamination with detailed illustrations and images taken with a scanning electron microscope, we transfer this species to *Draconarius* based on the presence of a dorsal apophysis on the conductor of the male palp, the position of the spermathecal head, and the shape of the genital opening of the female.

MATERIAL AND METHODS

Between 10 to 20 pitfall sites were established in the Seong lava cave on Jeju-do Island and in the surrounding forests (the Korean National Arboretum of Gwangreung, Gyeonggi-do; Mt. Odae National park, Gangwon-do) in Korea. At each site, two pitfall traps (plastic cups, height 6.3 cm, diameter 8 cm) were set 10 m apart (or 5 m inside the cave itself) and filled with ethylene glycol (Greenlade & Greenlade 1971). Drawings were prepared with an Olympus drawing tube, mounted on an Olympus SZX 12 and BX51 interference contrast microscope. The male palp was expanded by quick immersion (5 min) in concentrated KOH (0.2 g/ml H₂O) and specimens were fixed and preserved in 70% ethanol. Before dissection, the total body was drawn and body length measurements were made from whole specimens temporarily mounted in lactophenol. The genitalia of specimens were dissected in lactophenol, and the parts individually mounted in lactophenol under cover slips subsequently sealed with Glyceel or transparent nail varnish. If necessary, SEM photographs were used for the analysis of details. Scale bars in figures are in millimeters. All specimens examined in this paper will be deposited in the National Biological Resources Center (NBRC), Incheon City.

The descriptive terminology and spination of the legs follows that of Ono (1988) and Wang (2002). Abbreviations used are: a, apical; AER, anterior eye row; AIK, Arachnological Institute of Korea; ALE, anterior lateral eye; ALS, anterior lateral spinneret; AME, anterior median eye; d, dorsal view; ITA, intermediate tibial apophysis; p, prolateral view; PER, posterior eye row; PLE, posterior lateral

eye; PLS, posterior lateral spinneret; PME, posterior median eye; PMS, posterior median spinneret; r, retrolateral view; RTA, retrolateral tibial apophysis.

Family Amaurobiidae Thorell 1870

Subfamily Coelotinae

F.O. Pickard-Cambridge 1893

Draconarius Ovtchinnikov 1999

Type species.—*Draconarius venustus* Ovtchinnikov 1999, by original designation.

Draconarius coreanus

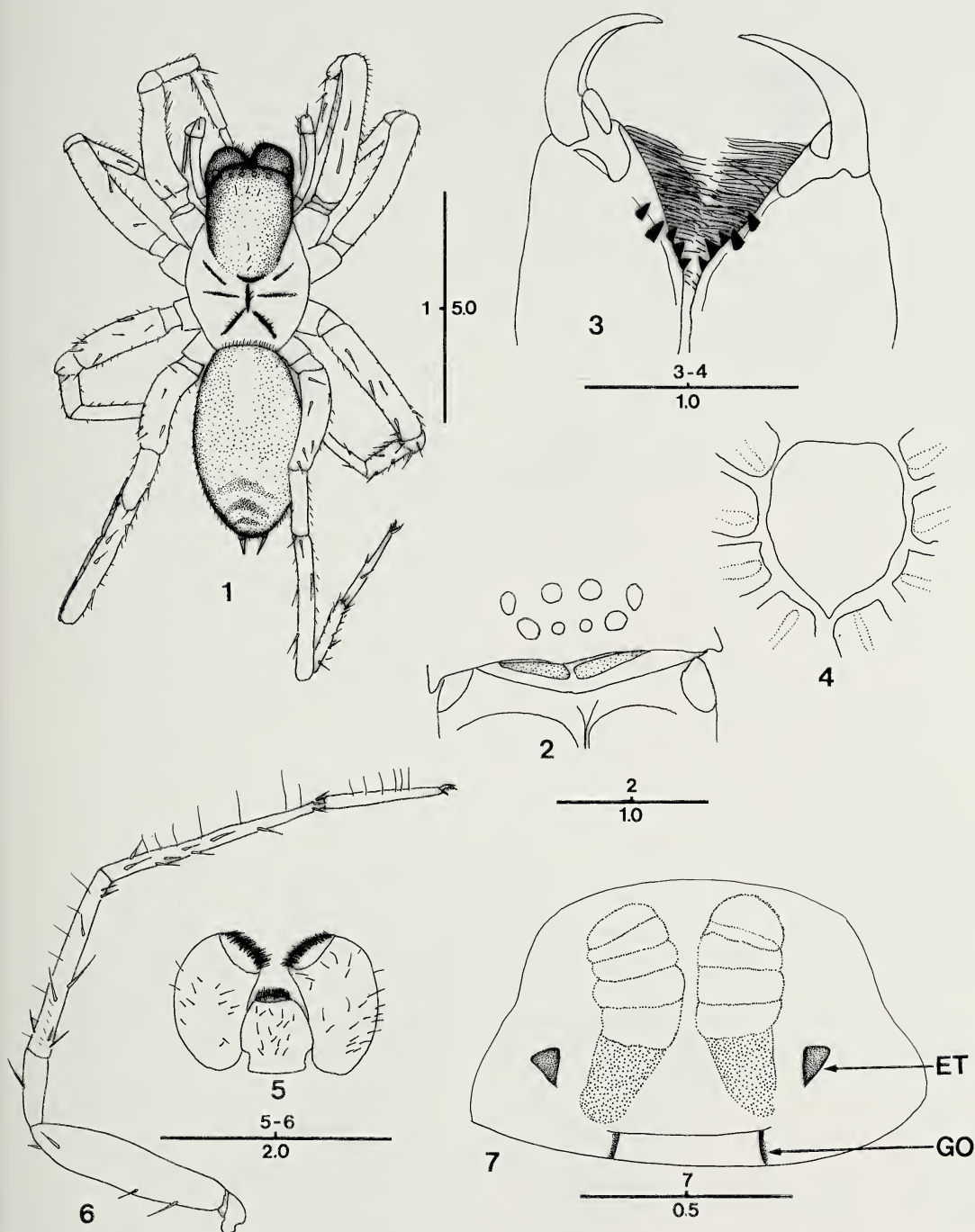
(Paik & Yaginuma 1969)

Figs. 1–19, 50, 51

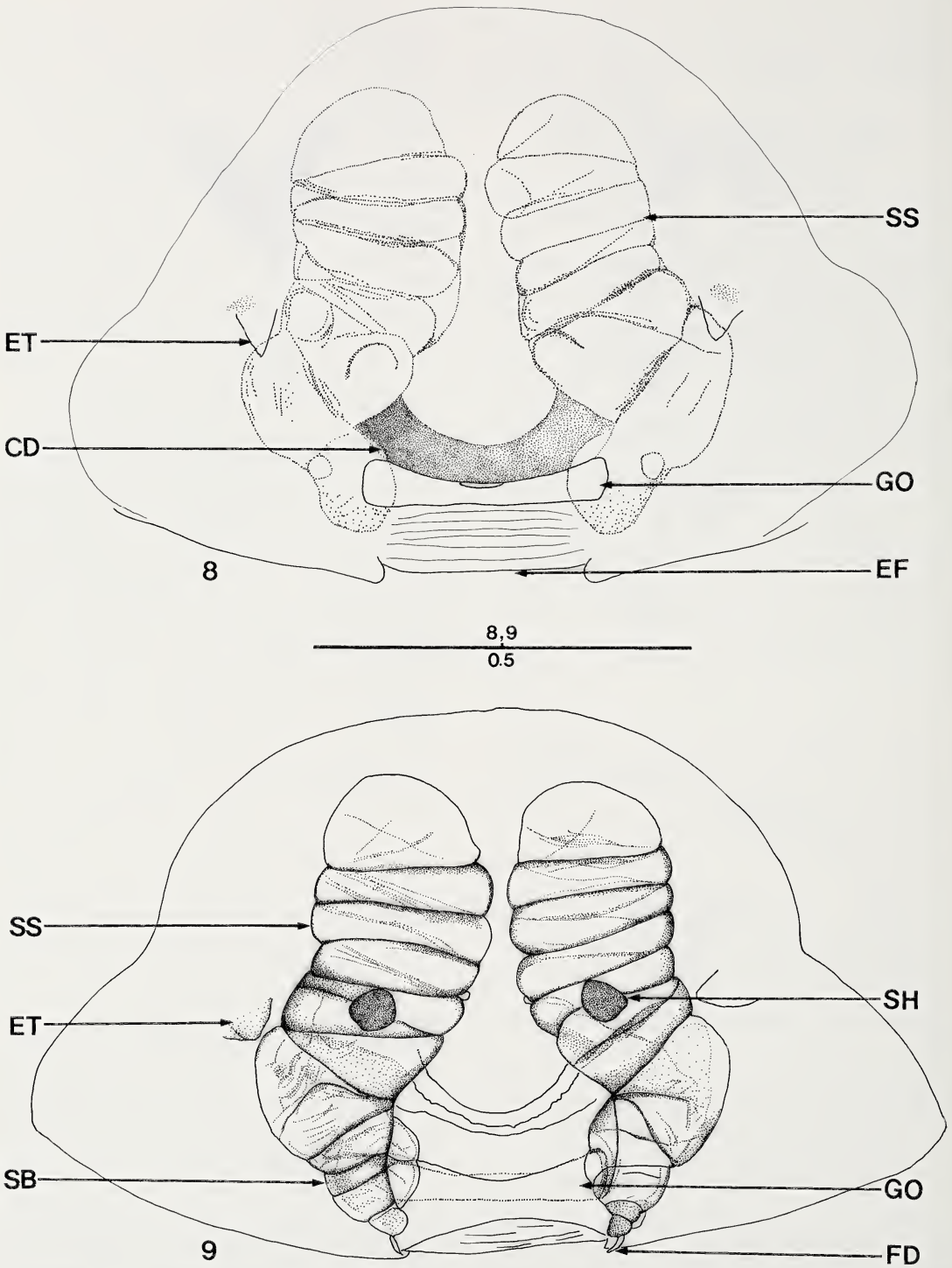
Coelotes coreanus Paik & Yaginuma, in Paik et al. 1969:837, figs. 62–64; Paik 1978:337, figs. 149.1–3; Namkung 2002:389, figs. 28.3a, b; Namkung 2003:391, figs. 28.3a, b.

Material examined.—KOREA: *Jeju-do*: 1 ♀, Seong lava cave, Sinchangri, Bukjeju-gun, 33°20'06"N, 126°11'10"E, 18 m, 17 January 2005, B.W. Kim (NBRC); 2 ♀, same location, 8 November 2003, B.W. Kim (NBRC); 1 ♂, same location, 9 August 1997, Y.G. Choi (NBRC).

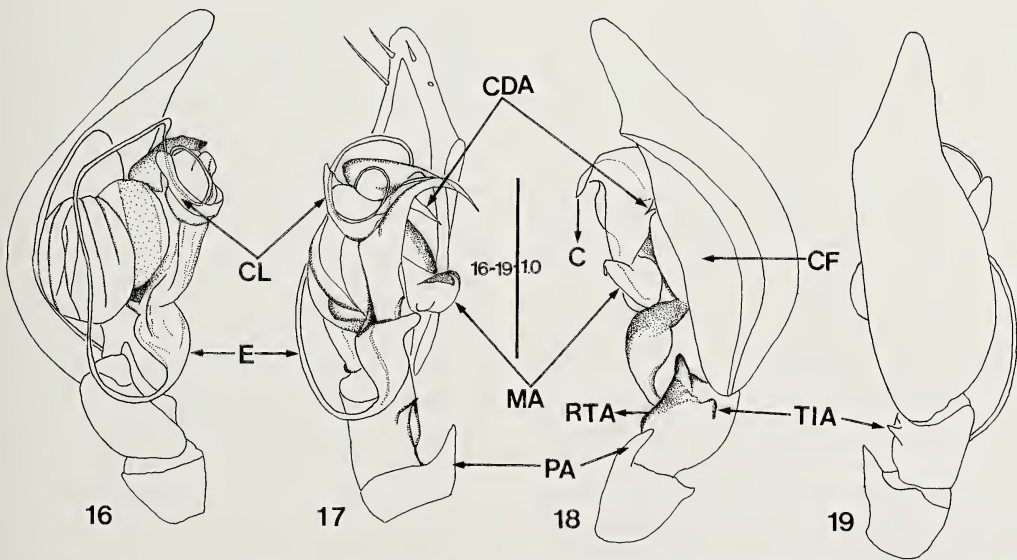
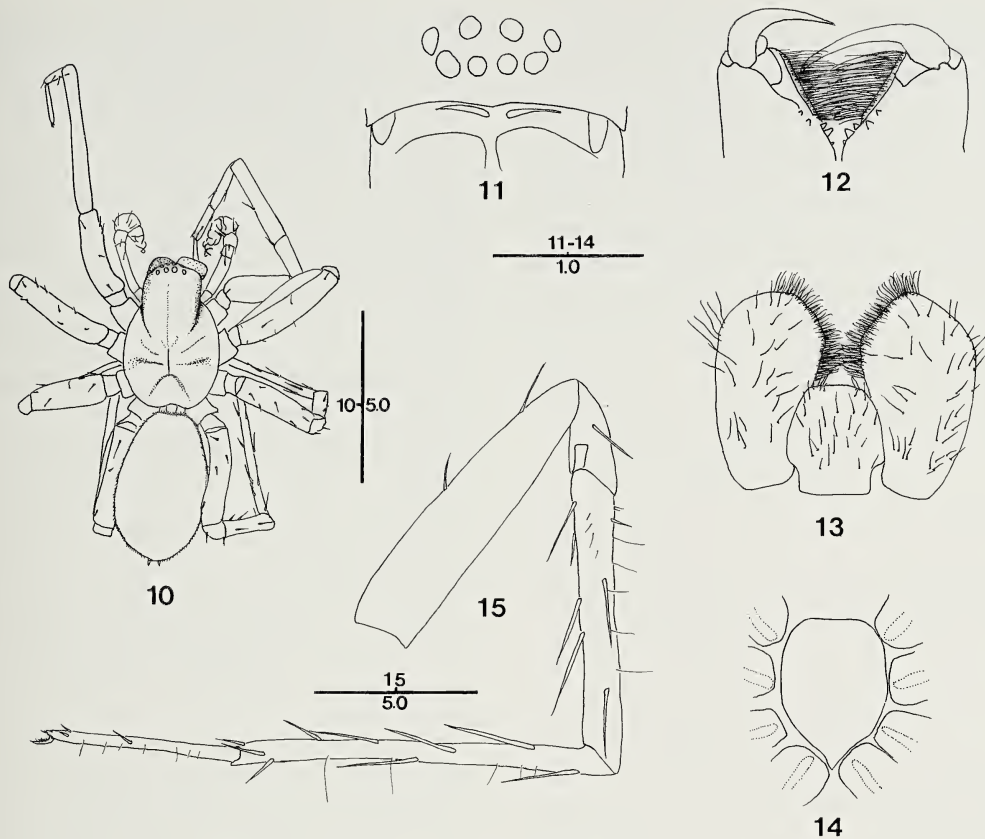
Diagnosis.—This species is similar to *D. kayasanensis*, *D. stemmleri* (Brignoli 1978), *D. wudangensis* (Chen & Zhao 1997) and *D. hallaensis* n. sp. in having the female epigynum with atrium (genital opening) very broadly rectangular, situated posteriorly near epigastric furrow, copulatory ducts short, and male palpal organs with cymbial furrow more than half cymbial length, and with large lamella on conductor. The species is easily distinguished by epigynal teeth separated more broader than both spermathecal margins (put between both spermathecal margins in *D. kayasanensis*), spermatheca cylindrical (expanded in *D. kayasanensis*), not attached distally (overlapping in *D. kayasanensis*), spermathecal heads small and circular, situated medially on spermathecae and cymbial furrow elongate, about 68% (83% in *D. kayasanensis*) as long as cymbium, conductor horizontally bent with modified sharp tip, conductor lamella large, median apophysis split distal end with inner part furrowed in the middle, (linear without inner part furrowed in *D. kayasanensis*; rounded in *D. hallaensis*), vague interior projection on the base (distinct in *D. kayasanensis*; fluent in *D. hallaensis*), and retrolateral tibial apophy-



Figures 1-7.—*Draconarius coreanus* (Paik & Yaginuma 1969) from Korea, female. 1. Habitus, dorsal view. 2. Eye area and clypeus, anterior view. 3. Chelicerae, posterior view. 4. Sternum, ventral view. 5. Endites and labium, ventral view. 6. 4th leg (left), prolateral view. 7. Epigynum, ventral view. ET = epigynal teeth, GO = genital opening.



Figures 8, 9.—*Draconarius coreanus* (Paik & Yaginuma 1969) from Korea, female. 8. Epigynum, ventral view. 9. Genitalia, dorsal view. CD = copulatory duct, EF = epigynal furrow, ET = epigynal teeth, FD = fertilization duct, GO = genital opening, SB = spermathecal base, SH = spermathecal head, SS = spermathecal stalk.



Figures 10–19.—*Draconarius coreanus* (Paik & Yaginuma 1969) from Korea, male. 10. Habitus, dorsal view. 11. Eye area and clypeus, anterior view. 12. Chelicerae, posterior view. 13. Endites and labium, ventral view. 14. Sternum, ventral view. 15. 4th leg (left), prolateral view. 16–19. Palp, left, prolateral, ventral, retrolateral, and dorsal views. CDA = conductor dorsal apophysis, C = conductor, CL = conductor lamella, CF = cymbial furrow, E = embolus, MA = median apophysis, PA = patellar apophysis, RTA = retrolateral tibial apophysis, TIA = tibial intermediated apophysis.

sis with sharp distal tip (rounded distal tip in *D. hallaensis*).

Description.—*Female*: medium sized spider 9.5 mm in length, slightly longer than male. Carapace elongated, moderately narrowed in eye area, and with distinct longitudinal medial fovea. Abdomen dark brown, with gray chevron patterns, heavily covered with short hair-like setae (Fig. 1). Palp three rows of trichobothria on tibia and 1 claw with 11 pectinate teeth. From dorsal aspect, AER more or less procurved, PER straight and AER slightly smaller than PER. AME smallest, other eyes roughly equal in size. Eye formula $ALE = PLE = PME > AME/ALE = PLE = PME > AME$. Clypeal height more than twice the AME; chilum divided (Fig. 2). Chelicerae with many long dense scopula hairs, 3 promarginal and 2 retromarginal teeth, condyle developed laterobasally and fang slightly longer than cheliceral width (Figs. 2, 3). Endite with anterior scopula, longer than wide; labium as long as wide (Fig. 5). Sternum shield-shaped, distinctly longer than wide, widest near coxa II, posterior end not protruding between hind coxae (Fig. 4). Legs without annulations (Figs. 1, 6): leg IV longest, leg III shortest; length of patella I + tibia I slightly shorter than carapace length; trochanters not notched; tibia with 4 rows of 4 to 7 trichobothria (leg I 7p-7d-5d-5r; leg II 5p-7d-4d-5r; leg III 5p-7d-5d-5r; leg IV 6p-8d-6d-5r), metatarsi with 1 row of 8 to 10 trichobothria, tarsi with 1 row of 8 to 10 trichobothria; tarsal organ situated close to distal end of tarsi, slightly anterior to distalmost trichobothrium; tarsi with 3 claws, upper claws with 11 pectinate teeth (13 in leg I), lower with 4 (3 in leg II).

Legs: leg formula 4123. Leg spination: leg I: femur with 5 spines, tibia with 7 spines (prolateral 0-1; ventral 2-2-2a), metatarsus with 8 spines (prolateral 1-1; ventral 2-2-2); leg II: femur with 6 spines, tibia with 8 spines (prolateral 1-1; ventral 2-2-2a), metatarsus with 10 spines (prolateral 1-2; retrolateral 0-0-1; ventral 2-2-2); leg III: femur with 7 spines, tibia with 11 spines (dorsal 1-0-0; prolateral 1-1; retrolateral 1-1; ventral 2-2-2a), metatarsus with 17 spines (dorsal 1-2-0; prolateral 1-1-2; retrolateral 2-0-2; ventral 2-2-2), tarsus with 4 spines (prolateral 0-1-1; ventral 0-1; retrolateral 0-1); leg IV: femur with 6 spines, tibia with 12 spines (dorsal 1-0-1; prolateral 1-1;

retrolateral 1-1; ventral 2-2-2a), metatarsus with 17 spines (dorsal 1-0-0, 1-0; prolateral 1-2-2; retrolateral 1-2-2; ventral 2-2-2), tarsus with 6 spines (prolateral 0-1-1; retrolateral 0-1-1; ventral 0-1-1).

Genitalia: Female epigynum and genitalia (Figs. 7–9) with short epigynal teeth slightly longer than wide, situated in the middle of epigynum, separated more broadly than both spermathecal margins; atrium (genital opening) very broadly rectangular, situated posteriorly near epigastric furrow; copulatory ducts short, broadly semicircular in shape, extending mesad of both epigynal teeth and originating posteriorly near epigastric furrow; spermathecae cylindrical, not attached distally; spermathecal heads small and circular, situated medially on spermathecae; spermathecal base a small complicated structure, situated on lateral margin of atrium; spermathecal stalk slender, not extended, situated side-by-side between both epigynal teeth; fertilization duct short, slender, underside situated close to epigastric furrow.

Male: medium sized spider 9.0 mm in length (Fig. 10), slightly smaller than female. Eye formula $ALE = PLE = PME > AME/ALE = PLE = PME > AME$. Clypeal height about twice AME diameter; chilum divided (Fig. 11). Chelicerae with many long dense scopula hairs, 3 promarginal, median tooth largest, 2 retromarginal teeth and small condyles at base and fang as long as wide (Fig. 12). Endite with anterior scopula, longer than wide; labium as long as wide (Fig. 13). Sternum shield-shaped, distinctly longer than wide, widest near coxae II, posterior end not protruding between hind coxae (Fig. 14). Legs (Figs. 10, 15) without annulations: leg formula 4123; tarsi with 3 tarsal claws, upper claws with 8 pectinate teeth (11 on leg I), lower claws with 2 (4 on leg IV); 4 rows of 2 to 6 trichobothria (leg I 6p-6d-2d-6r; leg II 6p-6d-6d-5r; leg III 6p-6d-5d-6r; leg IV 4p-6d-5d-4r), metatarsi with 1 row of 8 trichobothria, tarsi with 1 row of 8 trichobothria. Leg spination: leg I: femur with 8 spines, tibia with 7 spines (prolateral 0-0-1; ventral 2-2-2d), metatarsus with 8 spines (prolateral 1-1; retrolateral 0-0-1; ventral 2-2-1); leg II: femur with 7 spines, tibia with 8 spines (prolateral 0-1-1a; ventral 2-2-2a), metatarsus with 17 spines (dorsal 1-0-0; prolateral and retrolateral 1-0, 1-2-2; ventral 2-2-2), tarsus with

4 spines (prolateral 1-1; retrolateral 0-1; ventral 0-1); leg III: femur with 7 spines, tibia with 10 spines (dorsal 1-1; prolateral 1-1; ventral 2-2-2a), metatarsus with 10 spines (prolateral 1-2; retrolateral 1-1; ventral 2-2-1), tarsus absent; leg IV: femur with 6 spines, tibia with 10 spines (prolateral 1-1; retrolateral 1-1; ventral 2-2-2a), metatarsus with 16 spines (dorsal 1-0; prolateral and retrolateral 1-0, 1-2-2; ventral 2-2-2), tarsus with 5 spines (prolateral 1-1; retrolateral 0-1-1; ventral 0-1).

Male palp (Figs. 16–19, 50, 51) with 1 patellar apophysis; retrolateral tibial apophysis (RTA) long, about as long as tibia, broadly extended to the ventral part; intermediate tibial apophysis (ITA) small, grooved; cymbial furrow very elongate, about 68 % (1.5/2.2) as long as cymbial length, enclosing well developed concavity and with distal projection; conductor horizontally bent with modified sharp tip and slightly separated from lamella; conductor dorsal apophysis slender situated under conductor tip; conductor lamella large, modified with many small setules; embolus posterior in origin, extremely long linear, at least 2 times width of cymbium; median apophysis semicircular, split distal end with inner divided into 2 parts on the middle and vague interior projection on the base.

Dimensions (mm).—*Female*: Body length 9.5; carapace length 4.7, width 3.1, height 3.0; chelicera length 2.6, width 1.1, fang length 1.3; sternum length 2.5, width 1.9; endite length 1.5, width 0.8; labium length 0.7, width 0.7; clypeus height 0.2; AER 1.5, PER 2.0, AME 0.1, ALE 0.2, PME 0.2, PLE 0.2. Palp: femur 1.7, patella 0.7, tibia 1.0, tarsus 1.8, total 5.2. Leg I: femur 3.7, patella 1.6, tibia 3.0, metatarsus 3.0, tarsus 1.9, total 13.2. Leg II: femur 3.3, patella 1.6, tibia 2.5, metatarsus 2.7, tarsus 1.8, total 11.9. Leg III: femur 3.1, patella 1.5, tibia 2.2, metatarsus 3.0, tarsus 1.7, total 11.5. Leg IV: femur 4.0, patella 1.6, tibia 3.4, metatarsus 4.4, tarsus 2.0, total 15.4. Abdomen length 4.8, width 2.5, height 2.9. ALS 0.5; PLS 0.9 (0.5, 0.4).

Male: Body length 9.0; carapace length 4.1, width 2.9, height 3.3; chelicera length 1.8, width 0.9, fang length 1.0; sternum length 2.1, width 1.7; endite length 1.2, width 0.7; labium length 0.6, width 0.7; clypeus height 0.2; AER 1.2, PER 1.8, AME 0.1, ALE 0.2, PME 0.2, PLE 0.2. Palp: femur 1.5, patella 0.5, tibia 0.5, tarsus 2.2, total 4.7. Leg I: femur 3.5, patella

1.3, tibia 3.0, metatarsus 3.2, tarsus 1.9, total 12.9. Leg II: femur 3.3, patella 1.4, tibia 2.6, metatarsus 3.0, tarsus 1.9, total 12.2. Leg III: femur 3.3, patella 1.4, tibia 2.5, metatarsus 3.0, tarsus 1.9, total 12.1. Leg IV: femur 4.0, patella 1.4, tibia 3.4, metatarsus 4.7, tarsus 2.3, total 15.8. Abdomen length 4.5, width 3.0, height 3.3. ALS 0.5; PLS 0.9 (0.4, 0.5).

Distribution.—This species is known only from Seong lava cave, Jeju-do Island, Korea.

Remarks.—The specimens were found wandering on the lava surface of Seong lava cave.

Draconarius kayasanensis (Paik 1972)

new combination

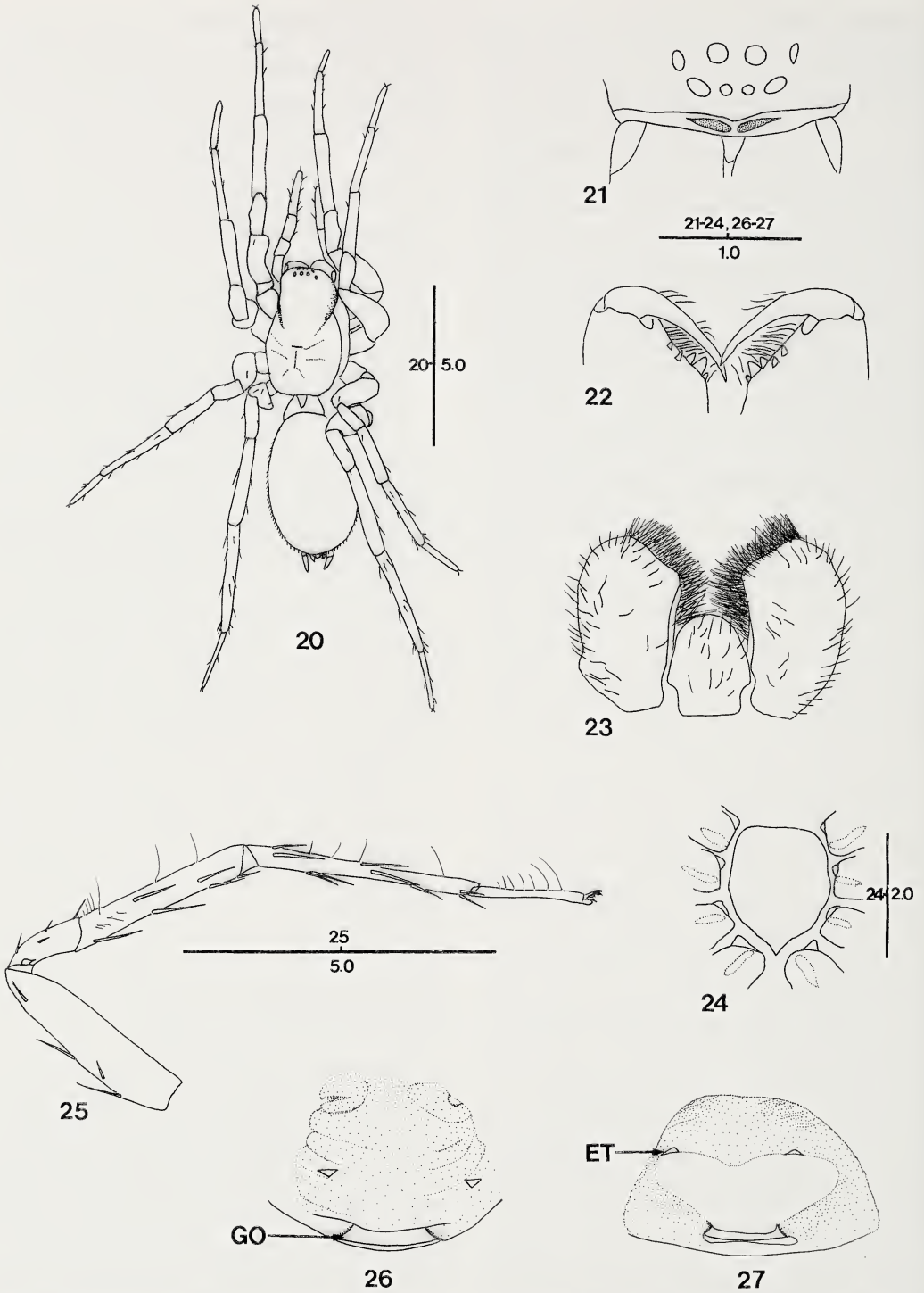
Figs. 20–39, 52, 53

Coelotes kayasanensis Paik 1972:49, figs. 1–7; Paik 1978:343, figs. 153.1–3.

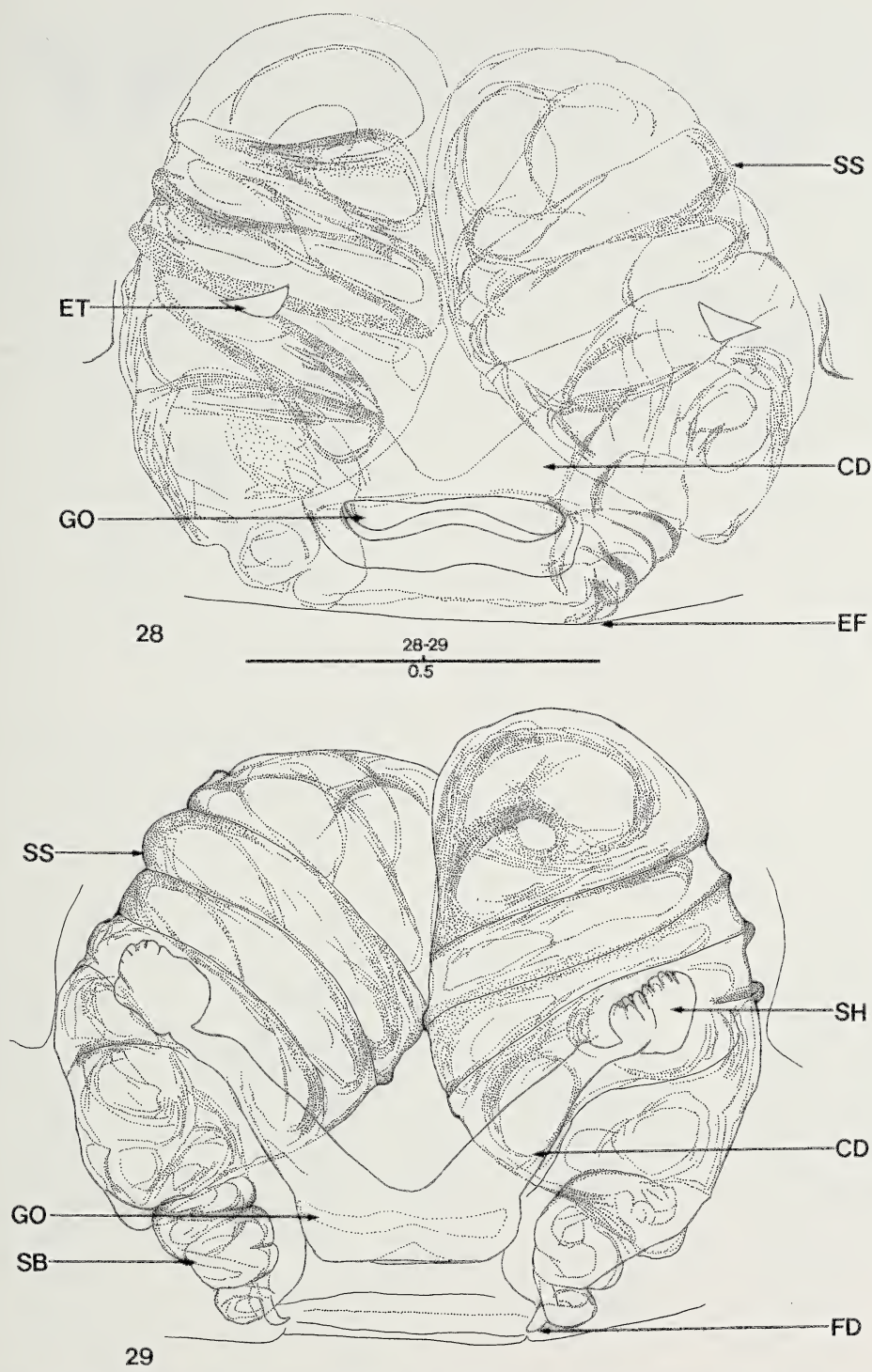
Ambanus kayasanensis (Paik 1972): Ovtchinnikov 1999:64; Wang 2003:27; Namkung 2003:396, fig. 28.10a; Namkung 2003:398, fig. 28.10a.

Material examined.—KOREA: *Gangwon-do*: 3 ♂, Gwangmijang in Mt. Odae, Gangreung City, 37°49'17"N, 128°38'16"E, 357 m, 10 June 2005, B.W. Kim (NBRC); 17 ♂, Mae Mountain summit in Mt. Odae, 37°45'35"N, 128°34'46"E, 1108 m, same date, B.W. Kim (NBRC); 1 ♂, 1 ♀, Temple Sangwon in Mt. Odae, Pyeongchang-gun, 37°47'00"N, 128°34'10"E, 839 m, same date, B.W. Kim (NBRC); 27 ♂, 1 ♀, same location, 11 June 2005, B.W. Kim (NBRC); 3 ♀, same location, 28 September 2005, B.W. Kim (NBRC); 2 ♂, same location, 11 October 2005, B.W. Kim (NBRC); 4 ♂, Temple Woljeong in Mt. Odae, Pyeongchang-gun, 37°43'48"N, 128°35'43"E, 662 m, 10 May 2005, B.W. Kim (NBRC); 2♂, same location, 11 October 2005, B.W. Kim (NBRC).

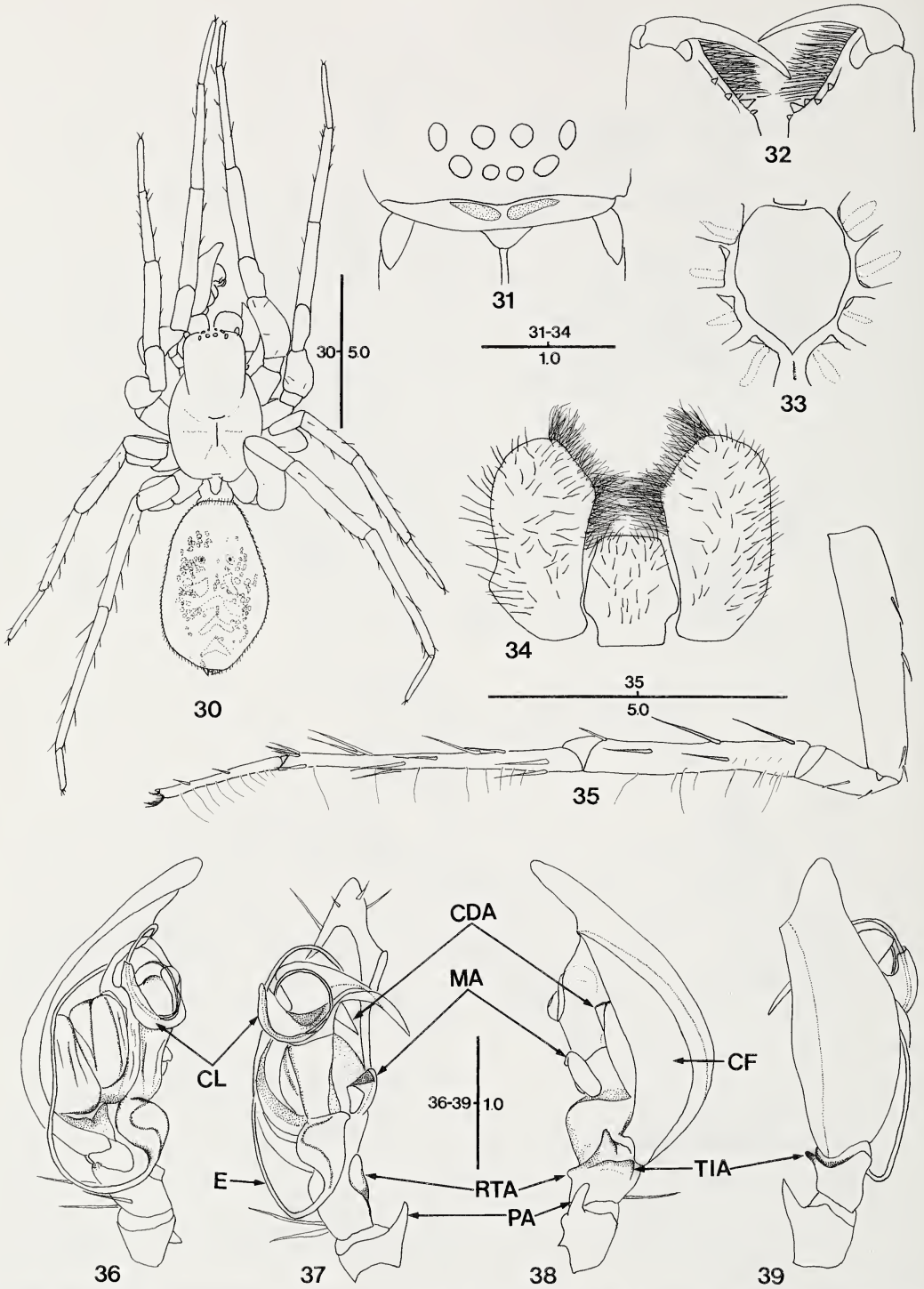
Diagnosis.—This species is similar to *D. coreanus*, *D. stemmleri*, *D. wudangensis* and *D. hallaensis* in having the female epigynum with atrium (genital opening) very broadly rectangular, situated posteriorly near epigastric furrow, copulatory ducts short, and male palpal organs with cymbial furrow more than half cymbial length, and a large lamella on conductor. The species is easily distinguished by the epigynal teeth situated along both spermathecal margins (separated more broadly than both spermathecal margins in *D. coreanus*), spermathecal heads spherical, spermathecal stalk expanded anteriorly (cylindrical in *D. coreanus*), overlapped, and cymbial furrow



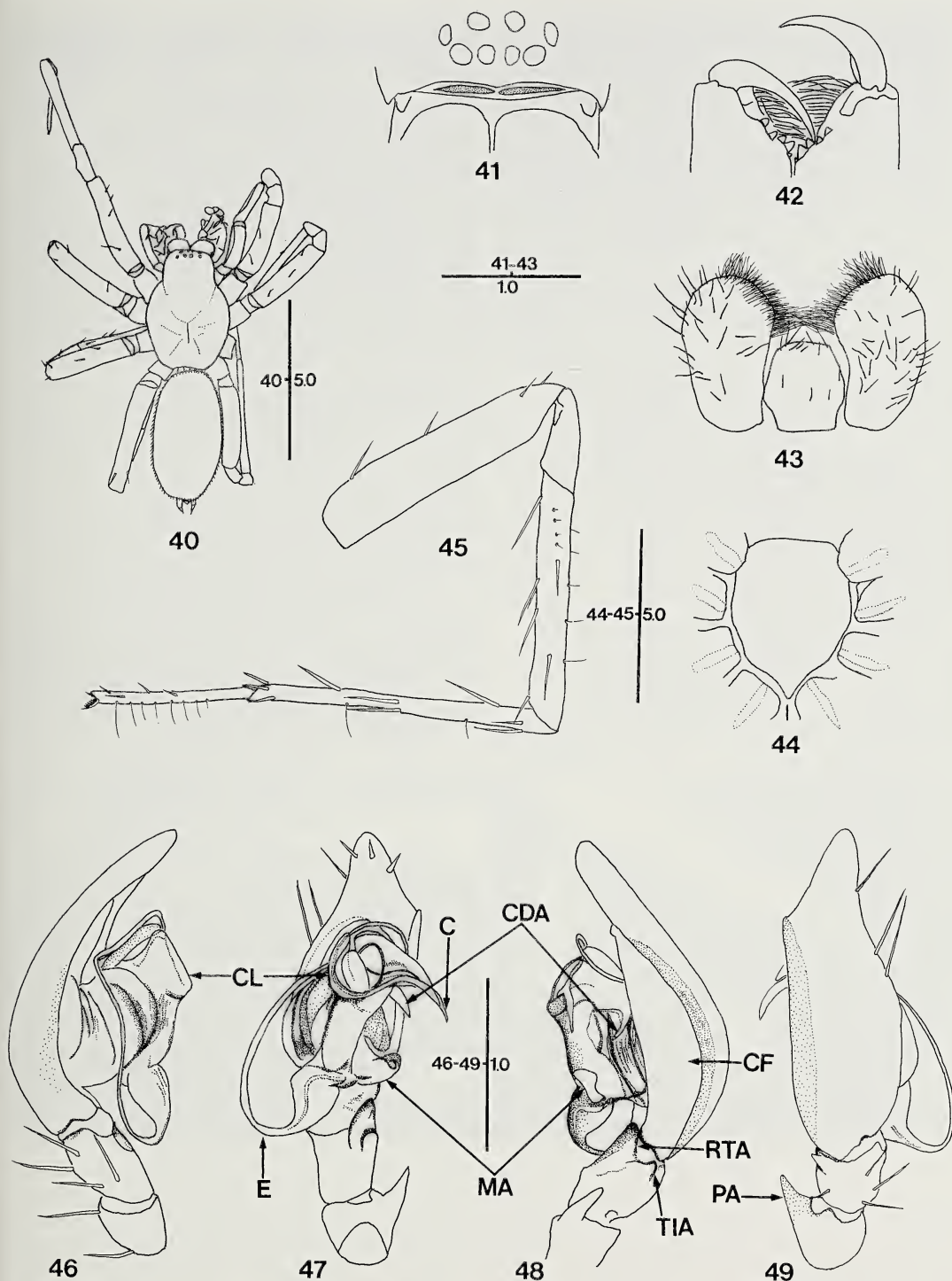
Figures 20–27.—*Draconarius kayasanensis* (Paik 1972) from Korea, female. 20. Habitus, dorsal view. 21. Eye area and clypeus, anterior view. 22. Chelicerae, posterior view. 23. Endites and labium, ventral view. 24. Sternum, ventral view. 25. 4th leg (left), prolateral view. 26. Epigynum, ventral view. 27. Epigynum, posterior view. ET = epigynal teeth, GO = genital opening.



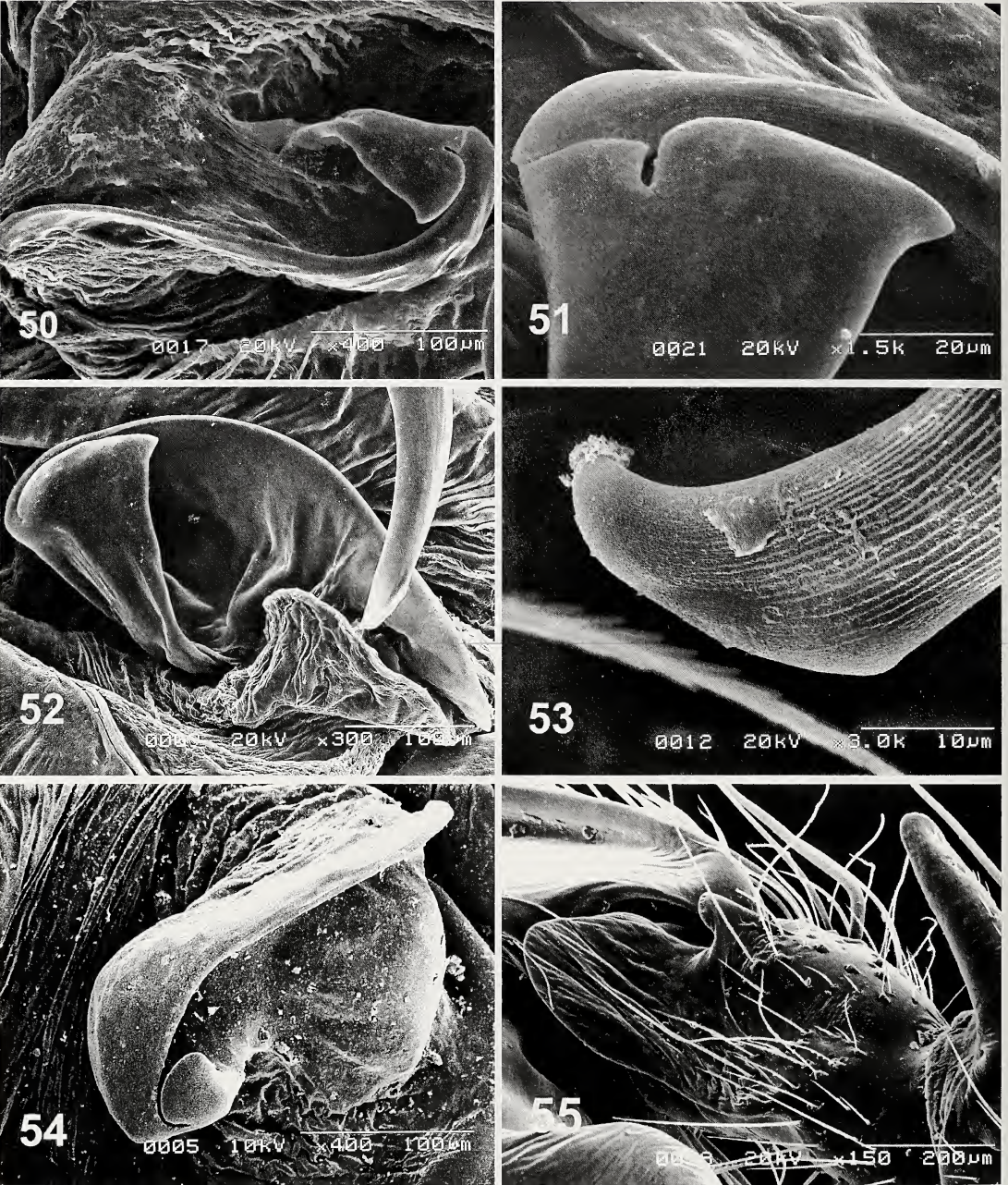
Figures 28, 29.—*Draconarius kayasanensis* (Paik 1972) from Korea, female. 28. Epigynum, ventral view. 29. Genitalia, dorsal view. CD = copulatory duct, EF = epigynal furrow, ET = epigynal teeth, FD = fertilization duct, GO = genital opening, SB = spermathecal base, SH = spermathecal head, SS = spermathecal stalk.



Figures 30–39.—*Draconarius kayasanensis* (Paik 1972) from Korea, male. 30. Habitus, dorsal view. 31. Eye area and clypeus, anterior view. 32. Chelicerae, posterior view. 33. Endites and labium, ventral view. 34. Sternum, ventral view. 35. 4th leg (left), prolateral view. 36–39. Palp, left, prolateral, ventral, retrolateral and dorsal views. CDA = conductor dorsal apophysis, C = conductor, CL = conductor lamella, CF = cymbial furrow, E = embolus, MA = median apophysis, PA = patellar apophysis, RTA = retrolateral tibial apophysis, TIA = tibial intermediated apophysis.



Figures 40–49.—*Draconarius hallaensis* n. sp. from Korea, male. 40. Habitus, dorsal view. 41. Eye area and clypeus, anterior view. 42. Chelicerae, posterior view. 43. Endites and labium, ventral view. 44. Sternum, ventral view. 45. 4th leg (left), prolateral view. 46–49. Palp, left, prolateral, ventral, retrolateral and dorsal views. CDA = conductor dorsal apophysis, C, conductor; CL = conductor lamella, CF = cymbial furrow, E = embolus, MA = median apophysis, PA = patellar apophysis, RTA = retrolateral tibial intermediated apophysis, TIA = tibial intermediated apophysis.



Figures 50–55.—SEM photographs of *Draconarius* species from Korea, male left palps. 50. *Draconarius coreanus*, male palp, left part, median apophysis. 51. *Draconarius coreanus*, male palp, left part, distal part of median apophysis. 52. *Draconarius kayasanensis*, male palp, left part, median apophysis. 53. *Draconarius kayasanensis*, male palp, left part, distal tip of embolus. 54. *Draconarius hallaensis* n. sp., male palp, left part, median apophysis. 55. *Draconarius hallaensis* n. sp., male palp, left part, retro-lateral tibial apophysis.

very elongate, about 83% (68% in *D. coreanus*) as long as cymbium, conductor roundly curved with modified sharp tip and distinctly separated from lamella on lateral margin, me-

dian apophysis thin semicircular, linear split distal end without inner part furrowed (with inner part furrowed on the middle in *D. coreanus*; rounded in *D. hallaensis*), distinct in-

terior semicircular projection on the base (vague in *D. coreanus*; fluent in *D. hallaensis*) and retrolateral tibial apophysis sharp distal tip (rounded distal tip in *D. hallaensis*).

Description.—*Female*: Medium sized spider 9.5 mm, distinctly smaller than male. Carapace elongated, moderately narrowed in eye area, and with distinct longitudinal medial fovea. Abdomen dark brown, without gray chevron patterns, heavily covered with short hairs (Fig. 20). Palp: with 3 trichobothrial rows on tibia; 1 claw with 8 pectinate teeth. From dorsal aspect, AER and PER straight, and AER slightly smaller than PER. AME smallest, others roughly same size. Eye formula $ALE = PLE = PME > AME/ALE = PLE = PME > AME$. Clypeal height twice as long as AME diameter; chilum divided (Fig. 21). Chelicerae with many long dense scopula hairs, 3 promarginal, median tooth largest, 2 retromarginal teeth, condyle developed laterobasally and fang slightly shorter than cheliceral width (Fig. 22). Endite with anterior scopula, longer than wide; labium as long as wide (Fig. 23). Sternum shield-shaped, longer than wide, widest near coxae II, posterior end not protruded between hind coxae (Fig. 24). Legs without annulations (Figs. 20, 25); leg IV longest, leg III shortest; length of patella I + tibia I slightly shorter than carapace length; trochanters not notched; tibia with 4 rows of 3 to 6 trichobothria (5p-5d-3d-5r on leg I, 3p-6d-5d-4r on leg II, 4p-6d-5d-5r on leg III, 5p-5d-5d-5r on leg IV), metatarsi 1 row of 5 to 7, tarsi with 1 row of 6 to 7; tarsal organ situated close to distal end of tarsi, slightly anterior of most distal trichobothrium; tarsi with 3 claws, upper claws with 10 (11 in leg II) pectinate teeth, lower claw with 4.

Leg spination: femur I with 7 spines, tibia with 7 (0-0-1 on prolateral; 2-2-2a on ventral), metatarsus 7 (0-0-1 on prolateral; 2-2-2 on ventral); femur II with 7 spines, tibia 8 (1-1 on prolateral; 2-2-2a on ventral), metatarsus with 10 spines (0-1-2 on prolateral; 0-1-0 on retrolateral; 2-2-2 on ventral); femur III with 6 spines, tibia 12 (1-0-1 on dorsal; 1-1 on prolateral and retrolateral; 2-2-2a on ventral), metatarsus 17 (1-0 on dorsal; 10, 1-2-2 on prolateral and retrolateral; 2-2-2 on ventral), tarsus 5 (1-1 on prolateral; 0-1-0 on retrolateral; 0-2 on ventral); femur IV with 6 spines, tibia 12 (1-0-1 on dorsal; 1-1 on prolateral and

retrolateral; 2-2-2a on ventral), metatarsus with 17 spines (1-0 on dorsal; 10, 1-2-2 on prolateral and retrolateral; 2-2-2 on ventral), tarsus with 6 (1-1 on prolateral; 0-1-1 on retrolateral; 0-2 on ventral).

Female epigynum (Figs. 26–29) with short epigynal teeth slightly wider than length, situated on both spermathecal margins; atrium (genital opening) very broadly rectangular, situated posteriorly near epigastric furrow; copulatory ducts short, broadly V-shaped, extending mesad of both epigynal teeth and originating posteriorly near epigastric furrow; spermathecal heads spherical, situated medially on spermathecae; spermathecal base small complicated structure, situated on the lateral margin of atrium; spermathecal stalk extended anteriorly, overlapped; fertilization duct short, slender, underside situated close to epigastric furrow.

Male: Medium sized spider 11.6 mm, distinctly larger than female. Eye formula $ALE = PLE = PME > AME/ALE = PLE = PME > AME$. Clypeal height more than twice AME diameter; chilum distinctly divided (Fig. 31). Chelicerae with many long dense scopula hairs, 3 promarginal, median tooth largest, 2 retromarginal teeth and small condyle at base and fang slightly longer than wide (Fig. 32). Endite with anterior scopula, longer than wide; labium as long as wide (Fig. 33). Sternum shield-shaped, longer than wide, widest near coxae II, posterior end not protruded between hind coxae (Fig. 34).

Legs without annulations (Figs. 30, 35): formula 4123, similar to female; tarsi with 3 tarsal claws, upper claws with 10 pectinate teeth (11 on leg I), lower with 3 (4 on leg IV); tibia with 4 rows of 5 to 7 trichobothria (leg I 7p-6d-6d-7r, leg II 5p-6d-5d-6r, leg III 5p-7d-5d-6r, leg IV 6p-5d-6d-6r), metatarsi with 1 row of 8 trichobothria (7 on leg III), tarsi with 1 row of 9 trichobothria (8 on leg I and 10 on leg IV). Leg spination: Leg I femur with 8 spines, tibia with 8 spines (ventral 2-2-2a; prolateral 0-1-1), metatarsus with 8 spines (ventral 2-2-2; prolateral 1-1); leg II: femur with 7 spines, tibia with 9 (prolateral 1-1-1; ventral 2-2-2a), metatarsus with 11 spines (dorsal 1-0-0; prolateral 1-2; retrolateral 1-0; ventral 2-2-2), tarsus with no spines; leg III: femur with 7 spines, tibia with 12 (dorsal 1-0-1; prolateral 1-1; retrolateral 1-1; ventral 2-2-2a), metatarsus with 16 spines (dorsal

1-0 on; prolateral and retrolateral 1-0, 1-2-2; ventral 2-2-1), tarsus with 4 spines (prolateral 1-1; retrolateral and ventral 0-1); leg IV: femur with 6 spines, tibia with 12 (dorsal 1-1; prolateral and retrolateral 1-1; ventral 2-2-2a), metatarsus with 17 spines (dorsal 1-0; prolateral and retrolateral 1-2, 2-2-2; ventral 1-2-2), tarsus with 5 (prolateral 1-1; retrolateral 0-1-1; ventral 0-1).

Male palp (Fig. 36–39, 52–53) with 1 patellar apophysis; retrolateral tibial apophysis (RTA) long, about same length as tibia, broadly extended to the ventral; intermediated tibial apophysis (ITA) small grooved; cymbial furrow very elongate, about 83% (2.0/2.4) as long as cymbial length, enclosing concavity, with distal projection; conductor roundly curved with modified sharp tip and distinctly separated from lamella on lateral margin; conductor dorsal apophysis slender situated under conductor tip; conductor lamella large, modified with many small setules; embolus posterior in origin, extremely long linear, at least 2 times width of cymbium, with terminal part injector-shaped; median apophysis thin semicircular, linearly split distal end without inner part furrowed on the middle, with distinct interior projection on the base.

Dimensions (mm).—Female: Body length 9.5; carapace length 3.9, width 2.6, height 2.3; chelicera length 1.7, width 1.0, fang length 0.6; sternum length 2.1, width 1.7; endite length 1.3, width 0.7; labium length 0.6, width 0.6; clypeus height 0.2; AER 0.8, PER 1.1, AME 0.1, ALE 0.2, PME 0.2, PLE 0.2. Palp: femur 1.4, patella 0.6, tibia 0.8, tarsus 1.5, total 4.3. Leg I: femur 3.0, patella 1.3, tibia 2.5, metatarsus 2.5, tarsus 1.6, total 10.9. Leg II: femur 2.8, patella 1.3, tibia 2.1, metatarsus 2.4, tarsus 1.6, total 10.2. Leg III: femur 2.5, patella 1.2, tibia 1.8, metatarsus 2.4, tarsus 1.4, total 9.3. Leg IV femur 3.3, patella 1.4, tibia 2.8, metatarsus 3.8, tarsus 1.7, total 13.0. Abdomen length 4.5/4.5, width 2.9/3.0, height 2.8/3.3. ALS 0.5/0.5; PLS 0.8/0.9 (0.4/0.4, 0.4/0.5).

Male: Body length 11.6; carapace length 4.1, width 2.9, height 3.3; chelicera length 1.8, width 0.9, fang length 1.0; sternum length 2.1, width 1.7; endite length 1.2, width 0.7; labium length 0.6, width 0.7; clypeus height 0.2; AER 0.7, PER 1.0, AME 0.1, ALE 0.2, PME 0.2, PLE 0.2. Palp: femur 1.5, patella 0.5, tibia 0.5, tarsus 2.2, total 4.7. Leg I: femur 3.5, patella

1.3, tibia 3.0, metatarsus 3.2, tarsus 1.9, total 12.9. Leg II: femur 3.3, patella 1.4, tibia 2.6, metatarsus 3.0, tarsus 1.9, total 12.2. Leg III: femur 3.3, patella 1.4, tibia 2.5, metatarsus 3.0, tarsus 1.9, total 12.1. Leg IV: femur 4.0, patella 1.4, tibia 3.4, metatarsus 4.7, tarsus 2.3, total 15.8. Abdomen length 4.5, width 3.0, height 3.3. ALS 0.5; PLS 0.9 (0.4, 0.5).

Distribution.—Mt. Odae, Gangwon-do, Korea.

Remarks.—The specimens were found wandering on the ground among stones and leaf litter.

***Draconarius hallaensis* new species**

Figs. 40–49, 54, 55

Draconarius coreanus (Paik & Yaginuma 1969): Wang 2002:67; Wang 2003:526, figs. 22C–E (males misidentified).

Material examined.—KOREA: *Cheju-do*: Holotype ♂, Mt. Halla, Seoguiipo City, 33°(18–20)'N, 126°(33–39)'E, Jeju-do Island, 12 August 1984, J.P. Kim (NBRC). KOREA: Paratypes: 4 ♂, same locality, 12 August 1984, J.P. Kim (NBRC); 12 ♂, Korean National Arboretum of Gwangreung, Pocheon city, 37°45'N, 127°10'E, Gyeonggi-do, 23 August 1994, K.S. Lee (NBRC).

Diagnosis.—This species is similar to *D. coreanus*, *D. kayasanensis*, *D. stemmleri* and *D. wudangensis* in having the male palpal organs with the cymbial furrow longer than half the cymbium length, median apophysis split distal end and a large lamella on the conductor. The species is also distinguished by its small size (less than 8 mm in total body length), cymbial furrow elongate, about 74% (68% in *D. coreanus*; 83% in *D. kayasanensis*) as long as cymbium, conductor horizontally bent with modified sharp tip, median apophysis semicircular, split distal end curved roundly in the inside, thumb-shaped inner part (with inner part furrowed on the middle in *D. coreanus*; linearly in *D. kayasanensis*), broadly fluent interior projection on the base (distinct in *D. kayasanensis*; vague in *D. coreanus*) and retrolateral tibial apophysis rounded distal tip (sharp in *D. coreanus* and *D. kayasanensis*).

Description.—*Holotype male*: medium sized spider, 7.8 mm. Carapace elongated, moderately narrowed in eye area, and with distinct longitudinal medial fovea. Abdomen dark brown, without gray chevron patterns,

heavily covered with short hairs (Fig. 40). From dorsal aspect, AER more or less procurved, PER straight and AER slightly smaller than PER. AME smallest, other eyes roughly equal in size. Eye formula $ALE = PLE = PME > AME$. Clypeal height slightly less than twice the AME; chilum divided (Fig. 41). Chelicerae with 3 promarginal, 2 retromarginal teeth, condyle developed laterobasally and fang slightly longer than cheliceral width (Fig. 42). Endite with anterior scopula, longer than wide; labium as long as wide (Fig. 43). Sternum shield-shaped, distinctly longer than wide, widest near coxae II, posterior end not protruded between hind coxae (Fig. 44). Legs: without annulations (Figs. 40, 45), leg formula 4123; leg IV longest, leg III shortest; length of patella I + tibia I slightly shorter than carapace length; trochanters not notched; tibia with 4 rows of 2 to 6 trichobothria (leg I 5p-2d-6d-2r, leg II 5p-4d-4d-4r, leg III 3p-6d-2d-4r, leg IV 4p-4d-3d-3r), metatarsi with 1 row of 2 to 6 trichobothria, tarsi with 1 row of 3 to 8 trichobothria; tarsal organ situated close to distalmost of tarsi, slightly anterior of distalmost trichobothrium; tarsi with 3 claws, upper claws with 10 pectinate teeth (8 in leg III and IV), lower claw with 2 (3 in leg III). Leg spination: leg I: femur with 6 spines (dorsal 1-1-2; prolateral 0-0-2), tibia with 7 spines (prolateral 0-0-1; ventral 2-2-2a), metatarsus with 8 spines (prolateral 1-1; ventral 2-2-2); leg II: femur with 5 spines, tibia with 7 spines (prolateral 0-1-1; ventral 1-2-2a), metatarsus with 9 spines (prolateral 1-1; retrolateral 0-1-0; ventral 2-2-2); leg III: femur with 6 spines, tibia with 10 spines (dorsal 1-0-1; prolateral and retrolateral 1-1; ventral 0-2-2a), metatarsus with 16 spines (prolateral and retrolateral 1-0, 1-2-2; ventral 2-2-2), tarsus with 4 spines (prolateral 1-1; retrolateral 0-1-0; ventral 0-0-1); leg IV: femur with 5 spines, tibia IV with 10 spines (prolateral and retrolateral 1-1; ventral 2-2-2a), metatarsus with 17 spines (dorsal 1-0-0; prolateral and retrolateral 1-0, 1-2-2; ventral 2-2-2), tarsus with 6 spines (prolateral and retrolateral 0-1-1; ventral 0-2).

Male palp (Figs. 46–49, 54, 55) with 1 patellar apophysis; retrolateral tibial apophysis (RTA) long, about same length as tibia, broadly extended to the ventral; intermediate tibial apophysis (ITA) small grooved; cymbial furrow very elongate, about 74% (1.4/1.9) as

long as cymbial length, enclosing concavity, with distal projection; conductor horizontally bent with modified sharp tip and slightly separated from lamella; conductor dorsal apophysis slender, situated under conductor tip; conductor lamella large, modified with many small setules; extremely long linear, at least 2X width of cymbium; median apophysis semicircular, split distal end curved roundly in the inside, thumb-shaped inner part, broadly fluent interior projection on the base and retrolateral tibial apophysis rounded distal tip.

Female: Unknown.

Dimensions (mm).—*Male:* Body length 7.8; carapace length 3.9, width 2.7, height 2.0; cheliceral length 1.6, width 0.8, fang length 0.9; sternum length 2.0, width 1.5; endite length 1.0, width 0.6; labium length 0.6, width 0.5; clypeus height 0.2; AER 0.6, PER 0.8, AME 0.1, ALE 0.2, PME 0.2, PLE 0.2. Palp: femur 1.4, patella 0.5, tibia 0.4, tarsus 1.9, total 4.2. Leg I: femur 3.1, patella 1.2, tibia 2.7, metatarsus 2.8, tarsus 1.8, total 11.6. Leg II: femur 2.9, patella 1.2, tibia 2.3, metatarsus 2.7, tarsus 1.7, total 10.8. Leg III: femur 2.7, patella 1.2, tibia 1.9, metatarsus 2.8, tarsus 1.5, total 10.1. Leg IV: femur 3.5, patella 1.3, tibia 3.0, metatarsus 4.0, tarsus 1.9, total 13.7. Abdomen length 4.0, width 2.3, height 2.3.

Distribution.—Korea (Korean National Arboretum of Gwangreung, Mt. Halla).

Remarks.—Specimens of this species were found wandering on the ground among stones and leaf litter.

ACKNOWLEDGMENTS

The authors wish to express their sincere thanks to Mr. J. Namkung and Dr. T.S. Kwon of the Korea Forest Research Institute, Prof. J.P. Kim of Dongguk University, Dr. C.H. Heo of the Korea National Park (KNP); and J.G. Kwon of Hanyang University, X.P. Wang of the University of Florida, USA, Dr. D.X. Song and Dr. J. Chen of Hebei University, China, and Dr. Y.M. Marusik of the Russian Academy of Sciences for providing several important papers and many valuable comments. Special thanks are due to Mark S. Harvey, Paula E. Cushing, and two anonymous reviewers, who helped improve the current work. This research was supported by grant 03-1-05-2-010 from the Korean Institute of Environmental Science and Technology (KIRST).

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Manuscript received 22 March 2006, revised 28 July 2006.

THE USE OF TREE-MOUNTED ARTIFICIAL SHELTERS TO INVESTIGATE ARBOREAL SPIDER COMMUNITIES IN NEW ZEALAND NATURE RESERVES

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ABSTRACT. Spiders have been advocated as valuable bio-indicators of forest ecosystem “health.” However, the numbers and types of spiders that are recorded at a site will usually be highly dependent on the sampling method employed. The use of lethal, indiscriminate invertebrate sampling techniques is undesirable when investigating rare species, or sampling within areas of high conservation status. Therefore we used non-lethal artificial tree-mounted shelters to monitor arboreal spiders in nature reserves near Christchurch, New Zealand. After three months, over 60% of the shelters had been used by spiders, increasing to 91% after twelve months. There were significant differences in the numbers of spiders found in the shelters at the different sites. However, factors such as the species of tree the shelter was attached to, ground vegetation, and levels of incident light did not affect the likelihood of a shelter being occupied. The species composition of the spider faunas in those sites regarded as high quality forest remnants was dissimilar to the faunas found in the low quality reserves. However, although spiders were more abundant in the high quality sites compared with the poorest stands of woodland, they were not more species rich. The shelters are inexpensive and easy to manufacture and are useful for long-term non-lethal monitoring of spider communities. They also have good potential as a tool for studying spider phenology, population dynamics, behavior, and as a collection/carriage device for live specimens used in conservation translocations.

Keywords: Arachnida, Araneae, monitoring, refuges, spiders, trees

INTRODUCTION

Spiders have been advocated as valuable surrogate measures for biodiversity assessment (Clausen 1986; Marc et al. 1999; Cardosa et al. 2004) and have been investigated for use as bio-indicators in natural and agricultural ecosystems and to monitor the progress of ecological restoration (e.g., Wheeler et al. 2000; Willett 2001; Longcore 2003; Perner & Malt 2003). The use of spiders as indicators of land and air poisoning by industrial processes or from misuse of agrochemicals has also been addressed (e.g., Madden & Fox 1997; Hodge & Vink 2000; Horváth et al. 2001).

When investigating populations or assemblages of spiders, the sampling method used has obvious repercussions for the numbers

and type of spiders that are collected (Work et al. 2002; Duffey 2004; Jiménez-Valverde & Lobo 2005; Meissle & Lang 2005). Although broad spectrum techniques such as pitfall trapping and chemical fogging of trees can provide substantial catches of spiders, these indiscriminate lethal trapping methods can prove counter-productive when investigating nature reserves or taxa of conservation importance. Non-lethal survey techniques, such as timed hand searches and standardized foliage beating can prove valuable in these circumstances since the sampler can be selective in determining which taxa, if any, are killed for further examination.

Non-lethal standardized samples of invertebrate assemblages have also been obtained

using "shelter traps" or "artificial retreats" (see Southwood 1978). For epigeal species, these shelters tend to be in the form of "cryptozoa boards"; flat pieces of timber or ceramic tiles placed on the ground, under which spiders (and other invertebrates) can take refuge (Bowie & Frampton 2004; Hodge & Standen 2006; Lettink & Patrick 2006). For arboreal spiders, Roberts (1985) and Jones-Walters (1989) describe the use of "bark traps" consisting of corrugated cardboard or plastic "bubble wrap" tied around the trunks of trees, the corrugations mimicking the convoluted surface of the tree bark and providing refuge for trunk-dwelling invertebrates. This technique has been used in some quantitative studies of spider behavior and community structure (Duffey 1969; Curtis & Morton 1974) and also in applied studies examining the influence of air pollution on arboreal spider assemblages (Horváth et al. 2001).

The current investigation originated from using tree-mounted wooden shelters to monitor and translocate rare endemic orthopteran insects ("weta"; Anostostomatidae and Rhaphidophoridae) in New Zealand nature reserves (Bowie et al. 2006). During the initial stages of the study, it was observed that the most common occupants of the shelters were spiders, including many with egg sacs and newly hatched spiderlings. It was decided to extend the investigation and continue to record the spiders residing in the shelters over the course of a year. This paper describes the numbers and types of spiders found, and examines whether various environmental factors (e.g., tree species, height, ground cover, etc.) affected shelter occupancy. The diversity and composition of the spider assemblages at each site were compared to establish whether these measures could be used to discriminate between high and low quality forest remnants and thus provide some indication of ecosystem "health" and of conservation/restoration success.

METHODS

The sampling methods have been described in detail in Bowie et al. (2006) but are given again here for clarity. The shelters were constructed from blocks of untreated pine wood (45 × 45 × 150 mm) cut with a 60° "roof" (Figure 1). A central groove (18 × 18 mm) was cut two-thirds down the length of the

block using a router. Transparent acetate was stapled over the groove as a window to enable the occupants to be viewed rapidly. Black polythene was then stapled over the window to prevent light from entering when the shelter was in position, and could be folded back to view any occupants when required. A plastic cover was nailed to the top of the shelter to reduce rain damage to the wood. The shelters were attached to trees using plastic-coated wire, so that the grooved side was firmly against the trunk of the tree. The height of the shelter from the ground was then recorded.

Fifty shelters were placed in each of six nature reserves in Canterbury, South Island, New Zealand: Hinewai Reserve (43.81687°S, 173.02254°E), Orton Bradley Park (43.67042°S, 172.71387°E), Quail Island (43.63103°S, 172.69008°E), Ahuriri Scenic Reserve (43.66375°S, 172.61782°E), Travis Swamp (43.48647°S, 172.68791°E) and View Hill (43.28676°S, 172.07572°E). These sites varied greatly in the plant species present and in the quality of the forest remnant. Quail Island is currently being ecologically restored and contained the poorest stands of native tree species, while Hinewai and Ahuriri are considered two of the finest forest remnants in Canterbury and have the most established and diverse stands of forest (Bowie et al. 2004, 2006; and refs. therein).

The shelters were attached to trees from August to October (spring) 2000 and checked at three-month intervals for 12 months. On the first three sampling dates, each shelter was scored for the presence/absence of adult and sub-adult spiders and their numbers recorded. The presence of egg sacs and batches of newly-hatched spiderlings were also recorded. On the final 12th month sampling date (spring 2001) all spiders were identified to species. Where possible this was done *in situ* but difficult specimens, juveniles and some voucher specimens were collected into 70% ethanol and returned to the laboratory to confirm identifications. Juveniles were assigned to a species if they could be confidently identified by unique non-genitalic characters and no other species of that genus were found at a particular site. Voucher specimens have been deposited in the Entomology Research Museum of Lincoln University, Canterbury, New Zealand. Nomenclature follows that of Platnick (2006).



Figure 1.—Female *Cambridgea* sp. with two egg sacs in a shelter at Travis Swamp.

During the summer sampling period, a number of environmental factors were measured for each shelter. These were: light intensity at the face of the shelter [Yokogawa lux meter, Yew 3281], moisture of the soil at the base of the tree [Hydrosense, Campbell Scientific, Australia], ground slope (using a clinometer), ground cover (i.e., percent area leaf litter, bare ground, vascular plants) and the depth of loose litter above firm soil. The effect of aspect was analyzed by classifying the ground slope and the shelters as facing north ($315\text{--}44^\circ$), east ($45\text{--}134^\circ$), south ($135\text{--}224^\circ$) or west ($225\text{--}314^\circ$). The effects of these various factors on the presence of spiders in a shelter (within each site and at any time dur-

ing the survey) were assessed using binary logistic regression or, for shelter aspect, the chi-square statistic.

RESULTS

Occupation of shelters.—Sixty-two percent of the shelters contained adult or sub-adult spiders after three months and the average level of occupancy increased gradually with time in the field (Table 1). Over the whole 12 month sampling period 91% of the 300 shelters contained live spiders on at least one occasion. Occupancy of the shelters varied significantly between the sites (Yates corrected $\chi^2 = 50.3$, $P < 0.001$, 5 *df*, based on presence of spiders in a shelter at anytime dur-

Table 1.—The proportion (%) of wooden shelters containing live spiders at each site on each sampling visit ($n = 50$; * = a small number of shelters were damaged by vandalism and contained zero spiders).

Time in field		Occupation of shelters (%)						
Months	Season(s)	Ahuriri	Hinewai	OB Park	Quail Is.	Travis Sw.	View Hill	Mean
3	Summer	76	68	72	28	66	62	62.0
6	Autumn	78	66	72	32	72	64	64.0
9	Winter	96	82	74	48	84*	52	72.7
12	Spring	88	88	92	40	78*	72	76.3
>12	All	96	100	100	64	94	92	91.0

ing the survey), with Quail Island shelters having consistently lower occupation than the other five sites (Table 1).

From 1200 shelter inspections, a total of 856 observations of live spiders were made. However, as the spiders were not marked it is not known whether some records represent repeat observations of the same individuals. The majority of occupied shelters (90%) contained only a single adult or sub-adult spider: there were 37 observations of two spiders together in a shelter and one observation each of three, four and five spiders cohabiting.

Factors affecting spider occupancy.—At each site, none of the environmental factors measured had a statistically significant effect on the likelihood of a shelter being occupied. There was also no association between occupancy and the direction the shelter was facing or the aspect of the ground slope.

Shelters were attached to a total of twenty-one tree species but there was no association between occupancy of shelters and tree species within each of the sites (analyzed using the G -statistic: $P > 0.1$ in all cases). From the high levels of occupancy observed it was apparent that shelters attached to all tree species used were acceptable to spiders. Differences in shelter occupancy on the same tree species occurred between sites. For example, shelters attached to kanuka trees (*Kunzea ericoides* (A.Rich.) J.Thompson) at Orton Bradley Park and Hinewai had 100% residency, whereas those at Quail Island, where occupation was lower in general, had spiders in only 50% of shelters.

The spider fauna.—A total of 243 spiders were recorded in the 300 shelters in the final (spring) sample, belonging to 21 species in 10 families (Table 2). Twelve species were represented by only a single specimen and only 11 of the 207 adults and sub-adults were

males. Other species were recorded in the shelters during the earlier samples but not found in the spring census. These were: *Eriophora pustulosa* (Walckenaer 1842) (Araneidae) at Quail Island and Travis Swamp, *Taieria kaituna* Forster 1979 (Gnaphosidae) at Ahuriri and Hinewai, and *Cambridgea peelen-sis* Blest & Vink 2000 (Stiphidiidae) at View Hill.

All of the species found are considered common in Canterbury, typically found on or around trees and foliage. Sixteen species are endemic to New Zealand, of which five are endemic to Canterbury and two endemic to Banks Peninsula (Forster & Wilton 1973; Blest & Vink 2000; see Table 2). An important finding was an adult male *Nuisiana arboris* (Marples 1959) (Desidae) in the winter samples at Orton Bradley Park, which had previously been known only from female specimens in New Zealand (Forster & Wilton 1973). *Neoramia janus* (Bryant 1935) (Agelenidae), *Theridion zantholabio* Urquhart 1886 (Theridiidae) and *Cambridgea ambigua* Blest & Vink 2000 (Stiphidiidae) laid numerous egg sacs in the shelters, many of which successfully produced spiderlings (Figure 1).

In terms of species composition, *Neoramia janus* was the dominant species contributing 42% of the spiders collected in the final sample, but was absent from both Quail Island and Travis Swamp. *Theridion zantholabio* was the most widespread species, being the only species to be found at all six sites. *Porrhothele antipodiana* (Walckenaer 1837) (Hexatheliidae) and *Cambridgea quadromaculata* Blest & Taylor 1995 (Stiphidiidae) were only found at the two least modified sites, Hinewai Reserve and Ahuriri Scenic Reserve. Conversely, *Achaeearanea veruculata* (Urquhart 1886) (Theridiidae) and *Cambridgea ambigua* were

found in high numbers but did not occur at these two high quality reserves.

The numbers of spiders recorded at the six reserves in the final spring sample reflected the overall patterns in occupancy, with Quail Island having fewer spiders than the other five sites ($\chi^2 = 15.6$, $P < 0.025$, 5 *df*). Orton Bradley Park recorded the greatest number of individuals, largely due to a seemingly disproportionate number of the theridiid *Theridion zantholabio*. The six reserves differed greatly in their degree of spider diversity and, although Quail Island had the lowest occupancy levels and smallest number of spiders, it had the greatest species richness, lowest dominance index and the highest Shannon-Wiener diversity index (Table 2). Indeed, four species were recorded only from Quail Island; *Clubiona huttoni* Forster 1979 (Clubionidae), *C. peculiaris* L. Koch 1873 (Clubionidae), *Hemicloea rogenhoferi* L. Koch 1875 (Gnaphosidae) and *Steatoda capensis* Hann 1990 (Theridiidae) (the latter two are introduced species). The two reserves considered to be the highest quality remnants, Ahuriri and Hinewai, actually had the lowest species richness, with only four and six species respectively.

Because only eight of the 21 species occurred at more than one location, comparing the "similarities" of the faunas is problematic. However, it is probably valid to regard the faunas found at the two high quality reserves, Ahuriri and Hinewai, as the most similar, as all four of the species found at Ahuriri also occurred at Hinewai, and both were dominated to a similar degree ($\approx 65\%$) by *Neoramia janus*. The spider assemblages found at the two poorest quality reserves, Quail Island and Travis Swamp, were disparate from those at the other four sites: they did not contain *N. janus* and both sites had a number of species that were not found at any of the other reserves.

DISCUSSION

Spiders readily inhabited the artificial shelters used in this study and their suitability as a domicile for spiders was further confirmed by the production of egg sacs and the successful emergence of spiderlings. None of the environmental factors measured affected the likelihood of shelter occupancy, and there was also no effect of tree species on the numbers of spiders found (but see Curtis & Morton

1974). We found no effect of height of the shelter on the trunk of the tree, although the height profile we used was limited to that within easy reach (by humans) from the ground. Placement of shelters higher up the trunk, or in the canopy, might reveal differences in occupation or use by different species.

Only 5% of the adult and sub-adult specimens found in the spring sample were male. Curtis & Morton (1974), in a survey of bark-dwelling spiders in Scotland, also found a bias towards female specimens in their bark-traps, but this contrasted with the sex ratio of the spiders they collected from the bark itself which had a strong male bias. It appears that females tend to remain sheltered while the males have a greater tendency to roam the more exposed areas of the tree trunk, possibly to locate females (Foelix 1996). A comparison of the spiders recorded in the shelters with those found on the surrounding bark would be informative on this issue. Also, in addition to taking samples from the bark surface, actively sampling spiders by foliage beating or hand searching would make it possible to place the assemblage of shelter-residents into a context of the arboreal fauna as a whole.

As a survey technique, it is conceded that the numbers and diversity of spiders recorded in the shelters were low compared to what might have been achieved with similar effort using more conventional sampling techniques. Although the number of species recorded was small, the shelters provided records of species that have not previously been found during intensive faunal surveys of these reserves (e.g., Quail Island and Travis Swamp; Macfarlane et al. 1998; Bowie et al. 2004). Rarefaction analysis of the spring data has indicated that further monitoring of the shelters, or the placing out of more sampling units, would likely locate further species at most sites, although it is possible that the shelters represent a novel habitat that is only ever likely to be used by a limited number of tree-dwelling species. The value of the shelters might lie in providing a non-lethal sampling method that complements other survey techniques within a particular site, and provides a standardized measure to compare resident spider faunas between sites.

The results of the spring survey allowed some interesting comparisons to be made.

Table 2.—Adult, sub-adult and immature spiders collected from 50 tree-mounted shelters at each site in the spring visit. ^E = endemic, ^I = introduced, ^C = Canterbury endemic, ^B = Banks Peninsula endemic.

		Ahuriri	Hinewai	OB Park
Agelenidae	<i>Neoramia janus</i> (Bryant 1935) ^{E, C}	29	30	22
	<i>Neoramia setosa</i> (Bryant 1935) ^{E, B}	—	—	1
Amphinectidae	<i>Maniho ngaitahu</i> Forster & Wilton 1973 ^{E, B}	—	1	—
Clubionidae	<i>Clubiona convoluta</i> Forster 1979 ^E	—	—	—
	<i>Clubiona huttoni</i> Forster 1979 ^E	—	—	—
	<i>Clubiona peculiaris</i> L. Koch 1873 ^E	—	—	—
Desidae	<i>Badumna insignis</i> (L. Koch 1872) ^I	—	—	—
	<i>Matachia</i> sp. ^E	—	—	—
	<i>Nuisiana arboris</i> (Marples 1959) ^E	—	—	3
Gnaphosidae	<i>Hemicloea rogenhoferi</i> L. Koch 1875 ^I	—	—	—
	<i>Taieria erebus</i> (L. Koch 1873) ^E	—	—	—
	<i>Gnaphosida</i> sp.	—	—	1
Hexathelidae	<i>Porrothoe antipodiana</i> (Walckenaer 1837) ^E	7	4	—
Orsolobidae	<i>Orsolobidae</i> sp. ^E	—	1	—
Salticidae	<i>Trite auricoma</i> (Urquhart 1886) ^E	—	—	—
Stiphidiidae	<i>Cambridgea ambigua</i> Blest & Vink 2000 ^{E, C}	—	—	—
	<i>Cambridgea quadromaculata</i> Blest & Taylor 1995 ^{E, C}	2	5	—
Theridiidae	<i>Achaeareana veruculata</i> (Urquhart 1886)	—	—	7
	<i>Rhomphaea</i> sp.	—	—	1
	<i>Steatoda capensis</i> Hann 1990 ^I	—	—	—
	<i>Theridion zantholabio</i> Urquhart 1886 ^E	6	5	22
	Total Spiders	44	46	57
	Trap occupancy (%)	88	88	92
	Species Richness	4	6	7
	Dominance, d	0.66	0.65	0.39
	Shannon-Wiener, H'	0.98	1.14	1.36

Quail Island is currently undergoing vigorous ecological restoration, with mature, native trees being few in number (Bowie et al. 2004) and this inferior quality of habitat was reflected in consistently low numbers of spiders being found and a spider assemblage with a very different composition from those found at the other sites. However, also of interest was that supposed high quality reserves at Ahuriri and Hinewai had the lowest number of species in the spring spider assemblages and that the species richness and species diversity at Quail Island were the highest of all six sites. This highlights a common problem when using summary diversity indices of animal assemblages to rank sites in terms of conservation value. It is sometimes not a case of *how many species* occur at a site but *which species* that provides the most sensible focus for site comparison.

The absence of some of the commoner species at Quail Island raises another potential use for the shelters: that of translocation of species between sites for conservation pur-

poses. For example, *Neoramia janus* was absent from Quail Island and Travis Swamp, the two most disturbed reserves, but was common in the other four sites. This species produced numerous egg sacs and batches of spiderlings within the shelters that could be used to establish populations in new locations. The animals could remain resident in the shelters during the transfer; the wooden shelters form a safe means of carriage for the animals and would likely reduce the incidence of transit mortality. By restricting the size of the entrance, predators such as rodents can be barred from entering the shelters.

The shelters have a number of other advantages over conventional (lethal) sampling methods. Regular inspection of the shelters can be used to monitor prey species and the rate of capture and, as there was generally only a single individual found in each shelter, there is potential for examining territoriality and the incidence of aggressive behavior towards non-residents. The shelters provide a method for investigating the phenology of the

Table 2.—Extended.

Quail I	Travis S	View H	Total	Adult	Sub adult	Immature
—	—	19	100	87♀	3♀ 4♂	6
—	—	—	1	1♀	—	—
—	—	—	1	1♀	—	—
—	1	—	1	1♀	—	—
1	—	—	1	1♀	—	—
1	—	—	1	1♀	—	—
—	1	—	1	1♀	—	—
—	—	1	1	1♀	—	—
—	—	4	7	4♀	—	3
1	—	—	1	1♀	—	—
—	—	1	1	1♀	—	—
1	1	—	3	—	1♀	2
—	—	—	11	8♀	1♀	2
—	—	—	1	1♀	—	—
—	1	—	1	1♀	—	—
1	24	6	31	23♀ 1♂	1♂	6
—	—	—	7	4♀	1♀	2
9	5	3	24	24♀	—	—
—	—	—	1	1♀	—	—
2	—	—	2	2♀	—	—
9	1	3	46	25♀ 1♂	1♀ 4♂	15
25	34	37	243	191	16	36
40	78	72	76			
8	7	7	21			
0.36	0.71	0.51	0.41			
1.58	1.05	1.48	1.88			

spiders in terms of temporal patterns in abundance and the production of egg sacs and spiderlings. Also, by marking individuals and visiting sites more regularly, there is the opportunity of obtaining information on individual mortality, site fidelity and migration.

In summary, these simple tree-mounted artificial shelters offer many opportunities for non-lethal study of arboreal spiders. In addition to providing a tool for long-term monitoring to evaluate the success of conservation management and site restoration, they can also be used to investigate various aspects of spider population dynamics, life history and behavior, and have good potential as a means of carriage during the translocation of species as part of ecological restoration programs.

ACKNOWLEDGMENTS

Thanks to Hugh Wilson, Bill Karaitiana (The Tawera Trust), Di Carter (Christchurch City Council), The Department of Conservation and the Quail Island Ecological Restoration Trust for allowing access to sites and for

their support. Thanks also go to Jill McCaw for help with sampling, the carpenters at Lineworks, Lincoln University, for shelter construction and to Ian Dawson for providing copies of the British Arachnological Society's papers. Two anonymous reviewers provided a number of helpful comments on an earlier draft of the paper.

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Manuscript received 24 April 2006, revised 14 December 2006.

THE FEMALE OF *PHRYNUS EXSUL* (AMBLYPYGI, PHRYNIDAE) FROM INDONESIA

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ABSTRACT. The female of *Phrynus exsul* Harvey is described from Rinca Island, Komodo Island National Park in the Lesser Sunda Islands, eastern Indonesia. The new populations were found in forested biotopes, suggesting that it occupies a range of habitats.

INTISARI. Betina *Phrynus exsul* Harvey dipertelakan dari Pulau Rinca, Taman Nasional Pulau Komodo di Kepulauan Lesser Sunda, Indonesia timur. Populasi baru ditemukan di kawasan hutan yang diduga sebagai perluasan habitat.

Keywords: Rinca Island, Komodo Island National Park, taxonomy, morphology, whip spider

The whip spider genus *Phrynus* Lamarck 1801 currently contains 28 living and two fossil species, with a further 4 species currently listed as *nomina dubia* (Quintero 1981; Armas & Gonzalez 2001; Armas & Viquez 2001; Harvey 2002, 2003; Armas & Gadar 2004; Poinar & Brown 2004; Teruel & Armas 2005) and most are distributed from the southern USA to northern South America (Weygoldt 2000; Harvey 2003). Recently, the first authentic member of the genus to be described from the Oriental region, *Phrynus exsul* Harvey 2002, was named from specimens collected from Flores Island in the Lesser Sunda Islands (Harvey 2002). The presence of a species of Phrynidae within the Wallacean region represents a major disjunction from North and South America where all other members of the genus reside. Harvey (2002) questioned whether *P. exsul* was an endemic Indonesian species or whether it might represent an accidental introduction, but the distinctive morphology suggested that it was not introduced. The only specimens of *P. exsul* available to Harvey (2002) were two male specimens collected from a cave near Labuhan Bajo in Flores Island. The recent collection of additional specimens of this species, including the first available female, from nearby Rinca Island, Komodo Island National Park allows us to ex-

tend the original description. It also allows us to add valuable distributional data and broaden the habitat preferences for this species.

METHODS

The specimens examined for this study are preserved in 96% ethanol and deposited in the Museum Zoologicum Bogoriense, Indonesia (MZB). The general terminology of the morphology and spination of pedipalps follows Weygoldt (1999, 2000), and the terminology of the pedipalps follows Harvey & West (1998) and Harvey (2002). The morphometric measurements follow Quintero (1981). The female genitalia was examined and illustrated by lifting the genital operculum. All observations and measurements were made with a stereomicroscope. Drawings were prepared with the aid of a drawing tube. All measurements are given in millimeters (mm).

The following abbreviations have been used to describe the trichobothria present on each segment (Weygoldt 1970): basitibia (bt = basitibial); distitibia (bf = basofrontal; bc = basocaudal; sbf = subasofrontal; stf = subterminofrontal; sbc = subbasocaudal; sc_{1-x} = series caudal and trichobothria present; sf_{1-x} = series frontal and trichobothria present).

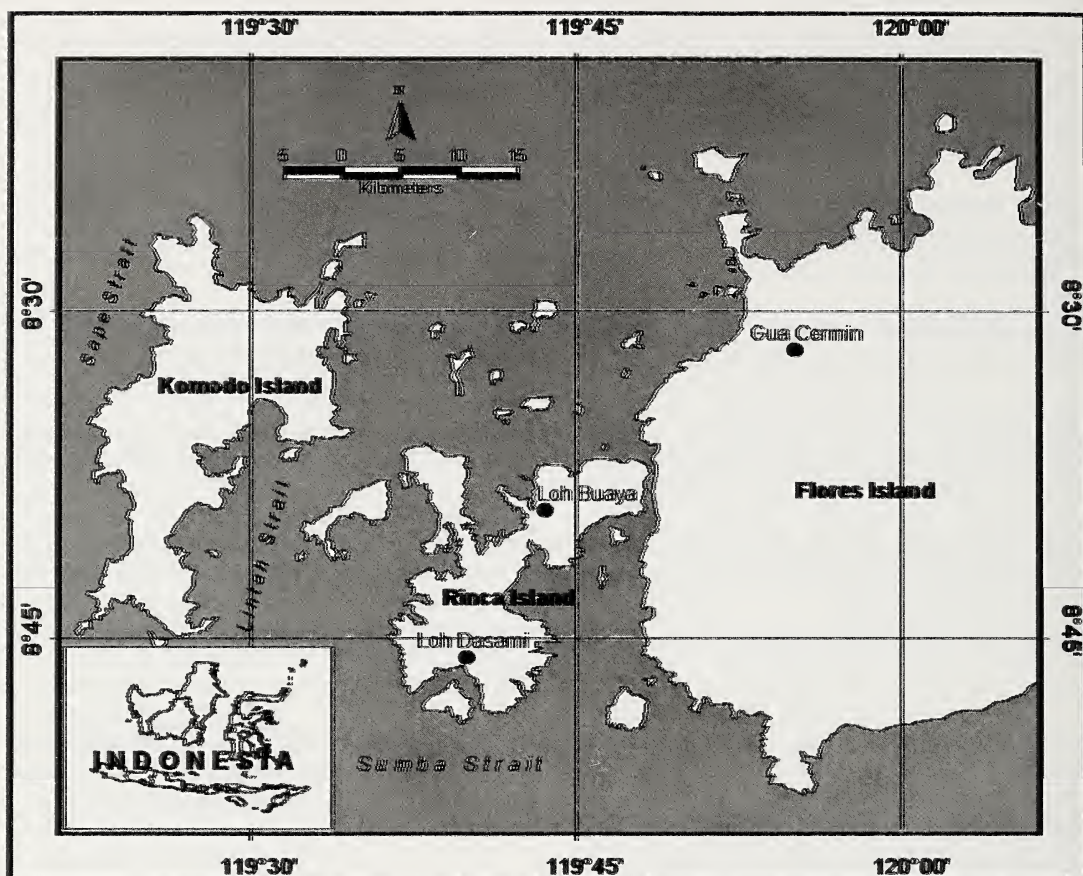


Figure 1.—Map showing the distribution of *Phrynus exsul* in Flores and Rinca Islands, Indonesia.

SYSTEMATICS

Family Phrynidae Blanchard 1852

Subfamily Phryinae Blanchard 1852

Genus *Phrynus* Lamarck 1801

Type species.—*Phalangium palmatum* Herbst, in Lichtenstein & Herbst 1797, by subsequent designation of Karsch (1879).

Remarks.—Members of the genus *Phrynus* have five principal spines on the pedipalpal patella and those of *Paraphrynus* have six principal spines (Weygoldt 1996). *Phrynus* is also distinguished from *Paraphrynus* by the relative length of the dorsal spines on the pedipalpal patella. *Phrynus* has a single spine between the two longest spines and *Paraphrynus* has two spines between the two longest spines. *Acanthophrynus* is distinguished from *Phrynus* and *Paraphrynus* by the presence of leaf-like setae on tarsus I that are lacking in *Phrynus* and *Paraphrynus*.

Phrynus exsul Harvey 2002

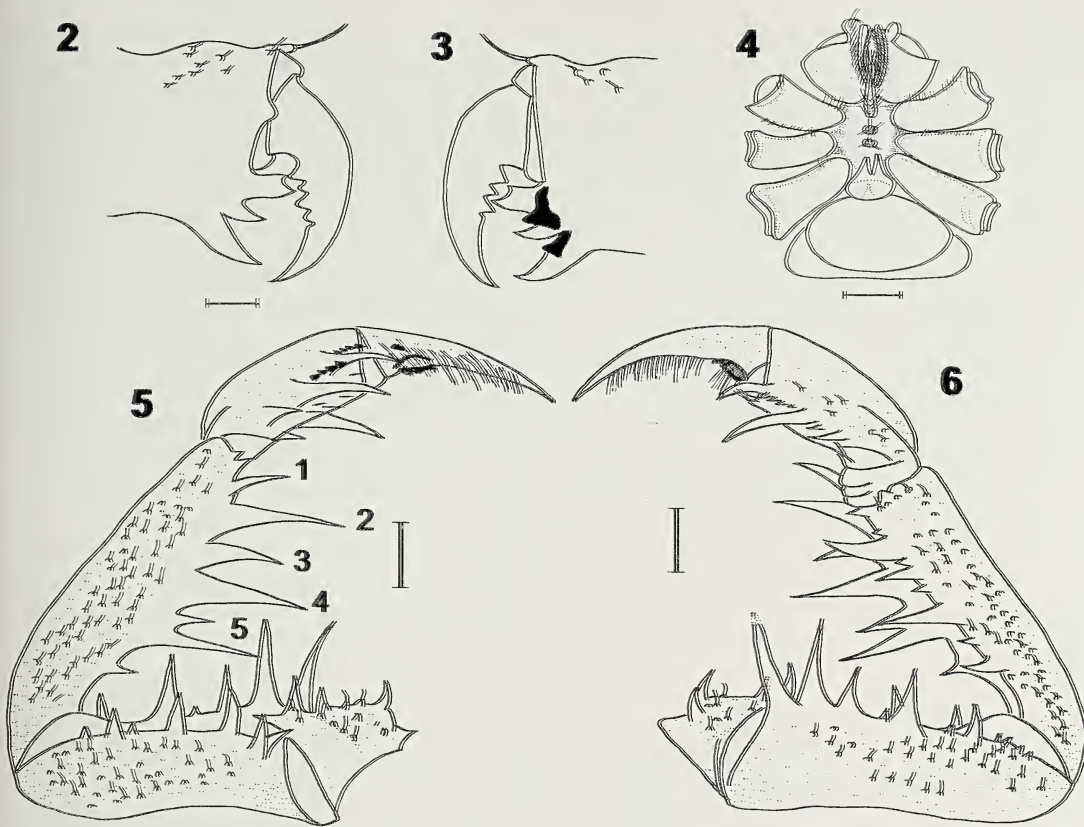
Figs. 1–10

Phrynus exsul Harvey 2002:471–473, figs. 1–6.

Material examined.—INDONESIA: *Nusa Tenggara Timur*: 1 ♀ (carrying eggs), Loh Dasami, Rinca Island, Komodo Island National Park, 8°46'21.3"S, 119°39'47.4"E, 14 August 2005, Arif Nurmawan (MZB, Ambl. 0107); 1 ♂, Loh Buaya, Rinca Island, Komodo Island National Park, 8°39'08.5"S, 119°43'12.1"E, 23 September 2005, Arif Nurmawan (MZB, Ambl. 0108).

Diagnosis.—*Phrynus exsul* differs from other species of *Phrynus* by the increased number of trichobothria on the distitibia, especially sbc and stf, which each have 5 trichobothria (Harvey 2002).

Description.—*Female*: Color: carapace, pedipalps and legs reddish-brown; tergites yellowish-brown; femur of legs have yellow



Figures 2–6.—Female *Phrynus exsul* from Loh Dasami: 2. Left chelicera, internal view; 3. Left chelicera, external view; 4. Cephalothorax and abdomen, ventral view; 5. Left pedipalp, dorsal view; 6. Left pedipalp, ventral view. (Scale bars: Figs. 2, 3 = 1 mm; Figs. 4–6 = 2 mm)

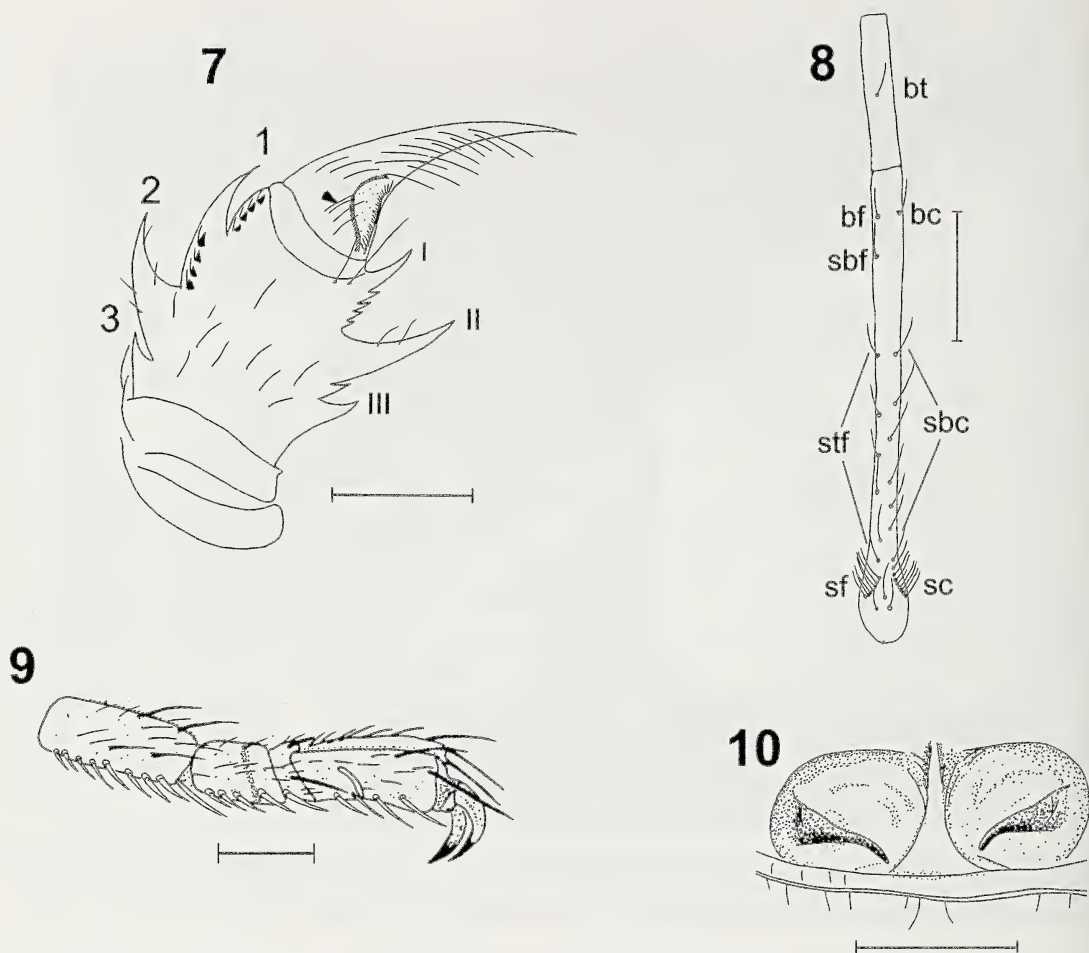
annulations, 3 brown and 2 yellow, clearly defined on leg IV. All seta acicular.

Carapace: anterior margin slightly concave, with several setiferous tubercles, eye tubercle black with eyes slightly facing antero-lateral margin, surface with many setiferous tubercles and small tubercles without setae, long sulcus present running from posterior to median eye to center of sulcus, 2 small sulci present on either side of long sulcus, central sulcus deep and radiating; frontal process concealed from above.

Chelicera (Figs. 2, 3): antero-dorsal surface of left chelicera on basal segment with well-developed setiferous tubercle on outer edge and some small setiferous tubercles, basal segment on internal margin with 3 teeth, the dorsalmost tooth bicusped, the lower cusp larger than the upper cusp, the lowermost the largest, the external margin with 3 teeth and 2 teeth on common base, movable hand with 4 large teeth and 1 very small tooth.

Sternum (Fig. 4): sternum tripartite and each sternite not expanded, anterior sternite with two stout distal setae, numerous smaller setae clustered on basal third, median and posterior sternite with 3 small setae.

Pedipalp (Figs. 5–7): pedipalps stout; trochanter antero-ventral with 4 major spines, antero-dorsal with 3 major spines and some setiferous tubercles; femur on antero-dorsal margin with 4 major spines and 2 minor spines, 5 major spines and 4 minor spines on antero-ventral margin, small bifid spine on distal edge; patella with 5 major spines and 2 minor spines on antero-dorsal margin, spine 5 with basal sub-spine about half of long major spine, spine 2 the longest and spine 1 the shortest, 4 major spines and 5 minor spines on antero-ventral margin; tibia with 3 spines on antero-dorsal margin, 4 denticles on upper spine 1, a row of 4 denticles on basal half of spine 1, antero-ventral margin with 3 spines, spine 2 the longest, 4 denticles between spine



Figures 7-10.—Female *Phrynus exsul* from Loh Dasami: 7. Left pedipalpal tibia, ventral view; 8. Left distitibia of leg IV; 9. Tarsus of left leg IV; 10. Female gonopods, dorsal view. (Scale bars: Figs. 9, 10 = 1 mm; Figs. 7, 8 = 2 mm)

1 and 2 and 1 denticle between spine 2 and 3; tarsus with single minute spine situated on dorsal surface of cleaning organ, cleaning organ with ventral row of long setae and dorsal row of smaller setae, apotele completely fused to tarsus (Fig. 7)

Legs (Figs. 8, 9): femora I, II, III and IV with small scales, distally pointed. Leg I with 30 tibial segments, 63 tarsal segments; femur I 2.38 times longer than carapace; femora II, III and IV with small tubercles and spines; tibiae II and III with 2 segments; tibia IV with 4 segments, third segment with 1 trichobothrium, bt (0.47), fourth segment (distitibia) with 35 trichobothria (Fig. 8), bc (0.10), bf (0.10), sbf (0.17), stf₁ (0.38), stf₂ (0.53), stf₃ (0.62), stf₄ (0.49), stf₅ (0.79), sbc₁ (0.39), sbc₂ (0.49), sbc₃ (0.56), sbc₄ (0.64), sbc₅ (0.70),

sbc₆ (0.75), number of trichobothria reduced in sf and increased in sbc compared to male specimen, distitibiae II and III with the same arrangement and number of trichobothria; tarsi legs II, III and IV with 4 segments, second segment with light transverse line on distal end, last segment with oblique slit; pulvilli absent (Fig. 9).

Genitalia (Fig. 10): female gonopod with claw-like sclerites, each hard and dark.

Measurements of female and male (mm) (male in parenthesis): Body length 28.00 (19.50). Carapace: median length 9.75 (6.25), width 14.5 (9.35), Median eyes to anterior margin 0.65 (0.4), lateral eyes to lateral eyes 4.60 (3.00), to anterior margin 2.00 (1.05), to lateral margin 2.00 (1.25). Pedipalps: trochanter length 4.50 (2.25), width 2.50 (1.60), fe-

mur length 9.00 (4.75), width 3.25 (2.40), patella length 9.50 (5.75), width 3.00 (2.80), tibia length 5.00 (3.00), width 2.50, tarsus length 5.00 (3.00). Leg I: femur 23.25 (15.00), patella 2.00 (1.00), tibia 43.00 (29.00), tarsus 54.50 (36.00). Leg II: femur 15.50 (10.00), patella 3.00 (1.50), basitibia 16.00 (9.00), distitibia 6.25 (4.50), metatarsus and tarsus 4.50 (2.75). Leg III: femur 4.50 (10.20), patella 3.00 (2.00), basitibia 17.50 (10.00), distitibia 7.25 (5.00), metatarsus and tarsus 5.00 (3.00). Leg IV: femur 14.50 (9.75), patella 2.75 (1.50), basitibia 16.00 (9.75), distitibia 7.00 (4.75), metatarsus and tarsus 5.00 (3.25).

Remarks.—The female of *P. exsul* is similar to the male from Loh Buaya and to the males originally recorded from the cave near Labuhan Bajo, Flores by Harvey (2002). The female differs from the males as the pedipalpal trochanter has 3 spines on the anterodorsal margin (4 spines in the males), and 4 spines on the anteroventral margin (5 spines in the males). Also, spine 5 on the dorsal margin of the pedipalpal patella of the female has the basal sub-spine about half the length of the major spine; this sub-spine is absent in the male. The presence of a basal sub-spine in spine 5 of the female specimen requires further investigation to determine if it represents sexual dimorphism or simply individual variation, as further female specimens are still unavailable.

The female gonopod is equipped with a hard, dark, claw-like sclerite, similar to that found in other phrynids (Weygoldt 1999; Perreti 2002), and which is considered to be autapomorphic for Phrynidae (Weygoldt 2000). The morphology of the female gonopods in Phrynidae shows very little variation between genera or species (Mullinex 1975; Quintero 1981; Weygoldt 1999, 2000).

Phrynus exsul was initially found in a cave near Labuhan Bajo, Flores, where they were reported to be very abundant (Harvey 2002). The two specimens from Rinca Island were taken from epigeal habitats indicating that *P. exsul* is not an obligate cavernicole. The female was found on a tree trunk in the rainforest and the male was collected on a rocky cliff. Several species of *Phrynus* are known to be troglomorphic, living both in caves and in epigeal habitats; the majority occur in epigeal habitats. No strictly cavernicolous species of *Phrynus* are known, in contrast to *Pa-*

raphrynus in which several troglomorphic species are known (Mullinex 1975, 1979; Quintero 1981).

Distribution.—*Phrynus exsul* was first recorded from Gua Cermin, Labuhan Bajo, Flores and is here recorded from Rinca Island, a part of Komodo Island National Park, situated slightly to the west of Flores Island (Fig. 1). The species may be more widely distributed within the Lesser Sunda Islands.

ACKNOWLEDGMENTS

We wish to thank Dr. Sri Hartini and Rochon Ubaidillah, Master of Philosophy, for their comments on an early version of the manuscript and Arif Nurmawan (Matalabio-gama, Faculty of Biology, Gadjah mada University) for his kindness in donating the specimens from Rinca Island which formed the basis for this study. Thanks also to Peter Weygoldt and Abel Pérez González for their comments, which helped to improve the manuscript.

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Manuscript received 2 May 2006, revised 2 November 2006.

INTERACTIONS BETWEEN THE SOCIAL SPIDER *ANELOSIMUS STUDIOSUS* (ARANEAE, THERIDIIDAE) AND FOREIGN SPIDERS THAT FREQUENT ITS NESTS

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ABSTRACT. Because competition for resources generally leads to the spatial exclusion of species using similar resources, it is surprising that foreign spider species are frequently observed in or near the nests of the social spider, *Anelosimus studiosus* (Hentz 1850) (Theridiidae). In this study, we quantified the frequency of *A. studiosus*-foreign spider co-occurrence and completed experiments designed to explain the nature of the host-foreign spider species associations. Four families were numerically prominent nest associates of *A. studiosus*: Salticidae, Anyphaenidae, Araneidae and Tetragnathidae. These families and the Agelemidae (intermediate association rate) and (Phidolomidae) (infrequent association rate) were subjected to further study. In choice trials, no foreign spider family discriminated nest silk or *A. studiosus*, itself, from the foliage the nest is built in. Predation events and maximum inter-individual spacing were significant outcomes of induced pair-wise interactions between host and foreign spiders for all families. Predation events were almost exclusively foreign on host. Field census results show that a close correspondence exists between the rate of loss of *A. studiosus* nests over time and the association rate of anyphaenids and agelemids at particular sites: these two families were the prominent predators on *A. studiosus* in laboratory trials. In reciprocal predation tests, juveniles suffered less predation in the presence of a mother; in the reciprocal trials, mothers also suffered less predation from foreign spiders when juveniles were present.

Keywords: Anti-predator behavior, intraguild predation, species co-occurrence

Organisms inhabit nests for many reasons, including not only the procurement of shelter from the physical environment, but also for refuge from predators, as an arena for mating and the rearing of broods, and as a site for foraging. Given the value of the nest sites themselves and energy applied to modification of them, it is not surprising that the host species encounters other species that intrude on its nests for a variety of reasons. This paper considers the extent to which foreign nest associates of a social spider species confer a benefit to the host versus a significant fitness cost.

In vertebrates such as fish and colonial nesting birds, increased protection against predators is an explanation that is frequently offered for the occurrence of mixed species nesting. There is evidence that colonial nesting among conspecifics confers similar antipredator effects in spiders (e.g., Uetz et al. 2002). How-

ever, the only known beneficial foreign nest associates to spiders are beetles and lepidopteran larvae that clean social spider nests of waste material (Robinson 1977; Furey & Riechert 1989). While many foreign spider species have been found to associate with social spider colonies, these have primarily been identified as either kleptoparasites that feed off of the webs of the host or as facultative commensals that build their own webs within the framework of the colony (reviewed in Buskirk 1981; see also Proctor 1992).

This study involves the spider *Anelosimus studiosus* (Hentz 1850) (Araneae, Theridiidae), which Brach (1977) categorized as a solitary species that offers extended maternal care of its young. Furey (1998) recently provided evidence that *A. studiosus* exhibits a mixed social strategy including solitary and communal nests at higher latitudes in the southeast US. Further documentation of the mixed strategy is presented in Jones et al. (in press). During the course of completing a lat-

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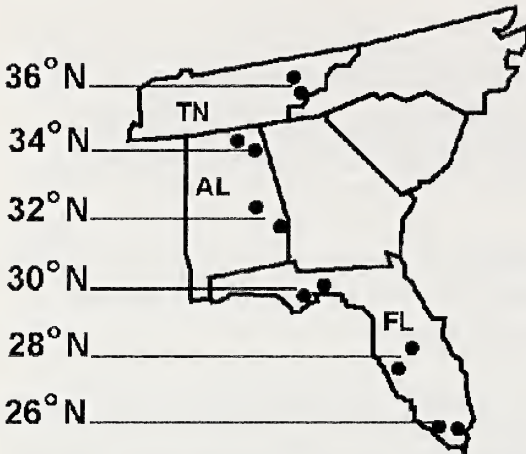


Figure 1.—Map showing latitudinal distribution of *Anelosimus studiosus* sampling locations.

itudinal study of the social structure of this species between south Florida and east Tennessee, we frequently found foreign spider species in its nests (also reported in Deyrup et al. 2004). In this paper, we quantify the frequency of co-occurrence of *A. studiosus* and foreign spiders in its nests and examine the nature of the association between the prominent foreign spider nest associates and the host species. In particular, we consider whether the foreign spiders are attracted to *A. studiosus* nests and whether the outcome of their association with *A. studiosus* is beneficial, neutral or costly to it.

METHODS

Frequency of nest invasion.—For every two-degree change in latitude between south Florida 26° and east Tennessee 36°, we established two independent 500 m transects along roadside or water-body edge vegetation at locations occupied by *A. studiosus* (Fig. 1). We collected 25 *A. studiosus* nests from each transect using a random draw method to determine the respective meter intervals from which to take a nest. A nest herein refers to silk bound leaves occupied by at least one *A. studiosus* individual. We collected nests coincident with the production of clutches by adult females at particular latitudes. We started the censuses in March at 26° and successively sampled higher latitudes through late spring into June. If we did not find a nest in a designated interval, we drew a new interval for that nest. If an interval had more than one

nest present, we chose the most centrally placed nest within that interval. We clipped each nest from the branch of the tree or shrub it was in and bagged it for return to our field laboratory for dissection. We recorded the number and age of *A. studiosus* individuals as well as the number of foreign spiders present by family. Voucher specimens were preserved in 70% ethanol for species determination. The remaining spiders were used as test subjects in the experiments described below. The voucher specimens are deposited in the Florida State Collection of Arthropods/Division of Plant Industry, Gainesville, Florida.

We made further nest collections throughout the study as test subjects were required for the various trials. These specimens were not collected from transect intervals but rather from nests collected in surrounding areas.

Based on the results of the nest censuses, we chose a number of families for further study. These included the Salticidae (jumping spiders) and Philodromidae (crab spiders), orb weavers belonging to the families Araneidae and Tetragnathidae, the sac spider family Anyphaenidae, and the funnel-web spider family Agelenidae.

Choice trials.—We completed two sets of trials to determine whether foreign spiders are attracted to some physical characteristic of an *A. studiosus* nest: Validation and Discrimination. The Validation test was performed to verify the assumptions that spiders will sample an arena environment and that they prefer containers with foliage to empty containers in a choice situation. In this simple test, we released a foreign spider into a hole at the top of a clear plastic tube (3 cm diam., 10 cm length) that connected two choice containers (clear plastic boxes of 10 cm diam. and 10 cm height). One of these containers was empty and the other contained a cluster of silk foliage that matched the leaf clusters *A. studiosus* occupies in the field. Upon release, the spider was watched for a 10-min interval in which its behavior was recorded. At the end of the 10-min watch period, we noted the location of the test subject within the arena system as in the Empty container, Foliage container or Connecting tube. The spider was then left within this arena system for 24 h. At this time, we again recorded its settling position as above. The containers, tubing and foliage clusters were cleaned between trials to

eliminate silk and chemical cues that might influence the path a new test subject might take. Forty-two *Agelenopsis emertoni* (Chamberlin & Ivie 1942) were tested in the Validation trials.

The Discrimination test was designed to determine whether a foreign spider's association with *A. studiosus* nests reflects an attraction to the host or merely reflects selection of similar plant physiognomy to that utilized by the host. The trials were completed in a three-chamber choice arena modeled after that used to test male choice of female reproductive states in Riechert & Singer (1995). The arena was constructed as described for the Validation test with the addition of intersecting tubes in the release area that permitted movement among three chambers offering the following choices: plant physiognomy (Foliage Only container), attraction to the silk nest produced by *A. studiosus* (Empty Nest container), or attraction to the host spider species, itself, (Occupied Nest container consisting of an adult female and her young). Identical artificial leaf clusters were available in all three choice containers. The Empty Nest and Occupied Nest treatments were established in a number of containers throughout the experiment. The contents of a natural nest collected in the field (generally a female and her young) were released into a chamber on the leaf cluster positioned in it. Once a web had been established in the leaf cluster, the chamber was ready for use in a trial. The host spiders were removed following establishment of the nest for containers used in the Empty Nest treatment. As in the Validation test, the settling location of each test spider was recorded after 24 h in the arena system and the containers and connecting tubes were cleaned between trials. Thirty choice trials were completed for the family Salticidae, 35 for the Anyphaenidae, 41 for the Araneidae, 30 for the Tetragnathidae, 19 for the Agelenidae, and 33 for the Philodromidae. Each test subject was used in only one trial.

Host spider-foreign spider interactions.—Because it is difficult to observe spider-spider interactions within foliage or the confines of a nest, we tested for possible interspecific interactions by releasing a foreign spider and an adult female host simultaneously into a clear plastic box measuring 10 cm on a side and 3 cm in height. This simple

arena test was used to gain some idea of whether the host and generally larger foreign spider (exception = some trials with philodromids) were indifferent to the presence of one another or exhibited avoidance as would be the case in territory defense or avoidance of predation. A square arena was used rather than a round one because spiders prefer corners for web and silk retreat construction. We left each pair of subjects in the box for a 24-h period. We then recorded: 1) whether a predation event occurred or not and if so, the direction of this event (host on foreign spider or foreign spider on host); and 2) the relative positions of the two individuals in the arena (if both survived) with reference to the box corners/sides: same corner/side, adjacent corners/sides, or opposite corners/sides. By chance, the two spiders were expected to settle 25% of the time on the same side, 25% of the time on the opposite side and 50% of the time on adjacent sides of the square arena (two times as many adjacent corner opportunities compared to other positions). Forty-five trials were completed utilizing salticids (mean \pm SE length = 6.1 ± 0.5 mm) as the foreign spider, 21 with anyphaenids (8.8 ± 0.2 mm), 15 with araneids (7.1 ± 0.5 mm), 15 with tetragnathids (8.0 ± 0.5), 11 with agelenids (8.4 ± 0.05), and 25 with philodromids (4.3 ± 0.08). *Anelosimus studiosus* averaged 3.0 ± 0.1 mm in length. Most of the foreign spiders used in these trials were collected from *A. studiosus* nests and the vegetation surrounding them.

Nest status censuses.—We marked 30 nests containing a brooding female at each study site within each latitude. We also recorded nearest neighbor nests in the vicinity of each focal nest: to the bottom, to the top, and to each side in the four compass directions (N, S, E, & W). This mapping protocol permitted us to distinguish between the total loss of a female and her brood and the construction of a new nest by the female at a nearby site over time; work with marked *A. studiosus* indicates that nest moves are of very limited distances (cm, Riechert & Jones unpublished observations). We checked these focal nests once a month over a 4-mo period for nest survivorship, extinction, and relocation.

Nest defense trials.—We completed two experiments testing for potential nest defense by *A. studiosus* against predation by other spider species. In the first, we tested for juvenile

survival in the presence of a predator under the two mother contexts (present vs. absent). In the second, we tested for mother survival under the two juvenile contexts (present vs. absent). As we completed each trial we recorded information on the instar of juveniles present (1st–5th). We completed a minimum of 50 trials of each context.

We collected single-female nests from the field for use in this experiment. We removed adult males and other individuals according to the treatment. We also removed juveniles of the desired age class in excess of five, maintaining this as a constant throughout the experiment. Each nest was then placed in a plastic container (10 cm diam. and height) and the nest composition treatment was maintained for 24-h prior to the introduction of a foreign spider.

Late instar and adult anyphaenids (mean \pm SE length = 8.9 ± 1.5 mm, range = 5.7–13.1 mm) were used as the predators in this experiment, as they showed the highest incidence of predation on *A. studiosus* in the interaction trials. After its collection from the field, each anyphaenid was maintained in the laboratory for 24 h before it was released into a box containing an *A. studiosus* nest. Upon removal of the foreign spider from the nest 24 hrs later, we recorded the number of surviving *A. studiosus* by type. Each *A. studiosus* nest and anyphaenid was used in only one trial.

RESULTS

Web censuses.—On average about a quarter of the dissected *A. studiosus* nests at every site contained foreign spiders (mean \pm SE proportion = 0.24 ± 0.03). Significant site and latitudinal variation existed in the frequency of foreign spider association with *A. studiosus* nests (chi-square tests, Site: $\chi^2 = 28.0$, $df = 11$, $P < 0.002$; Latitude: $\chi^2 = 20.5$, $df = 5$, $P < 0.001$). However, the results of a nested ANOVA (Latitude[site]) indicated that there was no significant latitudinal trend ($F = 1.23$, $P \approx 0.26$).

While the majority of the invaded *A. studiosus* nests had only one foreign spider, as many as five were found in a single nest. The means and standard errors presented in Table 1 for numbers of foreign spiders per invaded *A. studiosus* nest did not include spiderlings or egg sacs that were present in the case of a spider using the *A. studiosus* nest as a brood-

ing site. When more than one foreign spider was recorded at a given *A. studiosus* nest, 70% of the time they belonged to different spider families, a highly significant deviation from a chi-square expected ratio of 50:50 same vs. unlike family ($\chi^2 = 30.4$, $df = 1$, $P < 0.0001$). A nested (site within latitude) ANOVA was performed to test for geographic/habitat variation in mean number of foreign spiders per host nest; none was detected ($F = 1.06$, $P \approx 0.4$).

Ten spider families representing six different foraging strategies were found to frequent the nests of *A. studiosus* (See Table 1 for list of families and genera within families, associated foraging strategies, and the numerical representation of particular families at the respective sites). The familial association of nest invaders varied significantly among the sites (chi-square test, $\chi^2 = 71.0$, $df = 5$, $P < 0.001$). The ranking of taxon representation by site presented in Table 1 is in ascending order (most frequent [rank = 1]; least frequent [rank = 6]). Using these rankings determined for individual sites, we obtained an overall among site ranking for the foreign spider families found at *A. studiosus* nests. The Salticidae, Tetragnathidae, Araneidae, and Anyphaenidae were the most prominent nest associates overall. The Clubionidae and Agelenidae were intermediate frequency nest associates and the Philodromidae, Theridiidae, Dysderidae, and Mimetidae were infrequent nest associates. We used these results to select foreign spider families for inclusion in further studies. All of the prominent families listed above were included along with the Agelenidae, representing intermediate visitation frequency of association, and the Philodromidae representing infrequent association.

Choice trials.—In the two-choice Validation trials, 40% of the spiders were observed to visit both chambers during the course of the initial 10-min watch period and 88% ultimately settled within the container offering the foliage as opposed to the connecting tubing (7%) and Empty Container (5%).

The spider families tested in the Discrimination trials involving three chambers with varied levels of host cues differed significantly in the degree to which they settled in the choice arenas (minimally containing foliage) versus in the release location (network of tubes connecting the choice chambers) ($\chi^2 =$

Table 1.—Nest census results by latitude and site within latitude. *Spider Taxa. Orb Webs: Araneidae (1a): *Nuctemeca*, *Aramiella*, *Eriophora*, *Mangora*; Tetragnathidae (1b): *Tetragnatha*; Sheet-line webs: Agelenidae (2): *Agelennopsis*; Ambush Spiders: Thomisidae (3): *Misumenops*; Diurnal Hunters: Salticidae (4): *Hycia*, *Phidippus*; Nocturnal Hunters: Clubionidae (5a): *Clubiona*, *Trachella*, *Castianeira*; Anyphaenidae (5b): *Anyphaena*; Dysderidae (5c): *Dysdera*; Pirate Spiders: Mimetidae (6): *Mimetus*; Scattered-Line Webs: Theridiidae (7): *Argyrodes*, *Theridion*.

Latitude Site	Proportion Nests with Foreign Spiders	Mean + SE Number Foreign Spiders/Nest	Foreign Spider Taxa* #Ranked in order of decreasing abundance
26°			
Collier Seminole	0.36	1.17 + 0.11	¹ 3, ² 5a, ² 5b, ³ 1a, ³ 4
Miccosukee	0.35	1.35 + 0.19	¹ 1a, ² 4, ³ 1b, ³ 5a
28°			
Lake Manatee	0.33	1.28 + 0.12	¹ 1a, ² 1b, ³ 4, ⁴ 5a, ⁵ 5b, ⁶ 3, ⁶ 6, ⁶ 7
Lake Louisa	0.22	1.19 + 0.10	¹ 4, ² 1b, ³ 5a, ⁴ 1a, ⁵ 5b, ⁵ 6
30°			
St Marks	0.18	1.08 + 0.08	¹ 1b, ² 1a, ³ 5a, ⁴ 5b, ⁴ 4
Bottoms Rd	0.11	1.33 + 0.21	¹ 4, ² 5a, ³ 1b, ³ 2, ³ 5c
32°			
Lake Point	0.10	1.17 + 0.14	¹ 4, ² 1b, ² 2, ² 5a, ² 5b, ² 7
Wind Creek	0.33	1.47 + 0.26	¹ 1b, ² 1a, ³ 2, ⁴ 4, ⁴ 5a
34°			
Guntersville Lake	0.21	1.10 + 0.10	¹ 1a
Lake Weiss	0.16	1.10 + 0.10	¹ 4, ² 1a, ² 2
36°			
Melton Hill	0.16	1.0 + 0.01	¹ 1a, ² 2, ³ 1a, ³ 4, ⁴ 5a
Chillhowee	0.24	1.58 + 0.23	¹ 5a, ² 1a, ³ 2, ⁴ 1b, ⁵ 4, ⁵ 5b

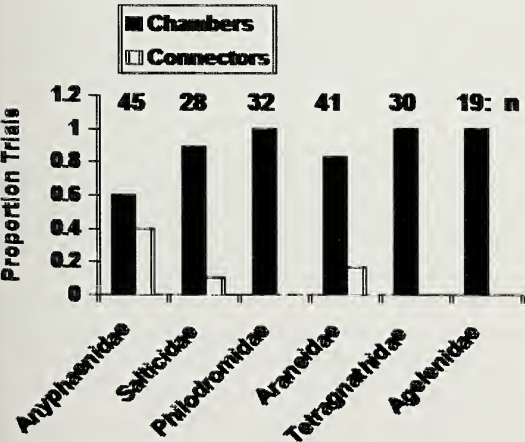


Figure 2.—Comparison of spider settling patterns by family in Discrimination choice trials: Chambers vs. in central tube area that radiated out to three chambers (Connectors). Number of trials indicated above bar for each family.

44.3, *df* = 5, *P* < 0.0001). The Anyphaenidae were the major contributors to this significant difference: 40% of them settled in the release area as opposed to in the chambers (Fig. 2). No significant differences were exhibited among the families in the particular chambers they settled in (Foliage Only, foliage with Empty Nest present, and foliage with Occupied Nest) (chi-square test for heterogeneity, $\chi^2 = 15.9$, *df* = 10, *P* ≈ 0.15) (Fig. 3).

Host spider-foreign spider interactions.—Thirty nine percent of the interaction trials involved a predation event. The results of an R by C chi-square test suggest that predation events were not evenly distributed among the spider families paired with *A. studiosus* ($\chi^2 = 15.5$, *df* = 5, *P* < 0.01). Inspection of the individual cells of the chi-square test contributing most to this significant test result identified the agelenid and anyphaenid trials; greater frequencies of predation events were observed than expected for these cells. The tetragnathids, and to a lesser extent the

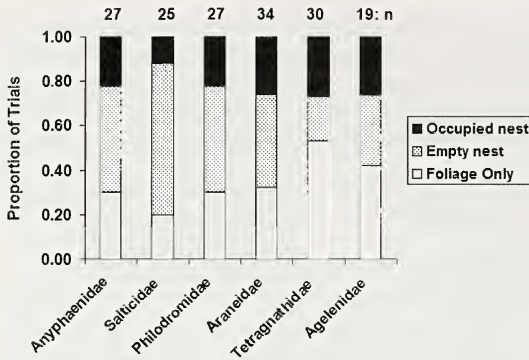


Figure 3.—Choices made among three chamber types by foreign spiders that frequent the nests of *A. studiosus*. All chambers had foliage present. Number of trials at top of bars. Chi-square test analysis of frequency distribution among families was non-significant.

salticids, also contributed to the significant chi-square test result. These latter families exhibited a lower frequency of predation events than expected. The majority of the predation events were in the direction of foreign spider on the host, *A. studiosus* (Fig. 4). The host preyed only on spiders from two families: Philodromidae and Salticidae.

With the exception of the trials involving tetragnathids, the settling patterns of surviving foreign spiders and *A. studiosus* in the square arena significantly differed from the random expectation of 25% same side, 50% adjacent side and 25% opposite side (Table 2). The high frequency of location at opposite ends of the arena contributed the most to the significant results in all but the araneid trials. In the case of this orb weaver, the exceptionally low number of close distances was the major contributing cell to the significant test result (Table 2).

Nest status censuses.—No focal nest relocations were detected. Comparison of the proportion of nests lost in the temporal censuses to the overall frequency of foreign spider associates recorded for the respective localities suggests that no significant relationship exists between foreign spider association with *A. studiosus* nests and nest extinctions ($R^2 = 0.06$; $F = 0.90$, $P \approx 0.36$). However, in restricting the comparison to the two spider families that exhibited high predation rates on *A. studiosus* in the interaction trials, (Anyphaenidae and Agelenidae; [Fig. 4]), we found a significant correlation to exist

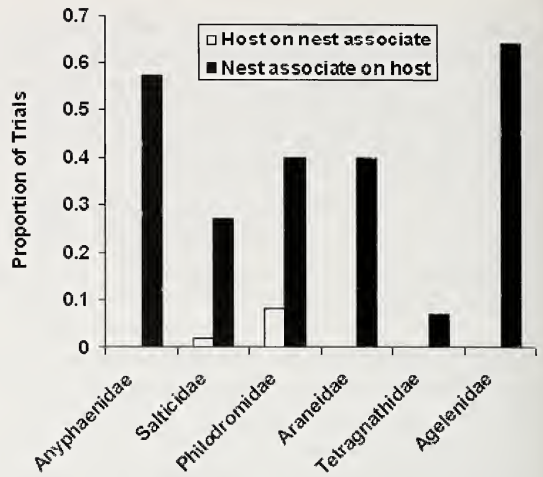


Figure 4.—Frequency of predation observed in host spider-foreign spider interaction trials.

between the frequency of nest association by spiders and nest extinction rate ($R^2 = 0.77$; ANOVA, $F = 31.2$, $P < 0.0002$; [Fig. 5]).

Nest defense trials.—No significant differences were observed in the frequencies of nests suffering predation relative to the instar of the juveniles present (range tested: instars 1-5) (chi-square test, $\chi^2 = 7.6$, $df = 4$, $P \approx 0.11$). Instar was thus pooled in the subsequent analyses under the category juvenile. In experiment 1, juveniles in nests with their mothers present suffered significantly less predation than they did in nests from which mothers were removed (chi-square test, $\chi^2 = 8.68$, $df = 1$, $P < 0.003$; [Fig. 6]). In experiment 2, the mothers suffered significantly less mortality from predators when they had juveniles present compared to when they did not

Table 2.—Foreign spider-host spider relative position (%) in square chamber at end of interaction trials. *Chi-square test results significant at 0.05 after Bonferroni correction. Cells contributing greatest value to test results in bold type.

Associate Family	Same side/corner	Adjacent side/corner	Opposite side/corner
<i>Expected %</i>	25	50	25
Salticidae*	11.6	25.6	62.8
Tetragnathidae	14.3	57.1	29.6
Araneidae*	6.7	40.0	53.3
Anyphaenidae*	4.8	23.8	71.4
Agelenidae*	0	9.1	90.1
Philodromidae*	4.0	24.0	72.0

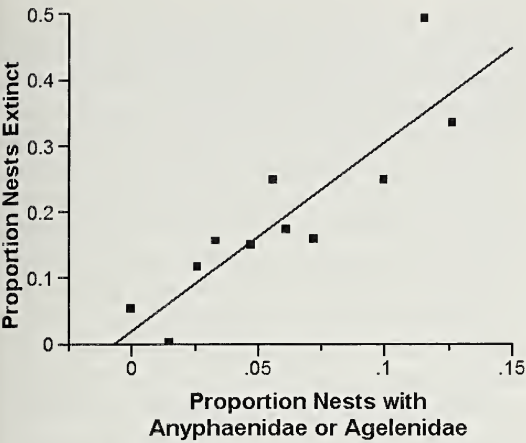


Figure 5.—Relationship between rates of nests lost in temporal nest censuses at 12 localities (two replicates at latitudes: 26°, 28°, 30°, 32°, 34°, & 36°) and rates of nest association by Agelenidae and Anyphaenidae in initial nest census at these sites ($R^2 = 0.77$).

have young (chi-square test, $\chi^2 = 5.44$, $df = 1$, $P < 0.02$; [Fig. 6]). Finally an ANOVA comparing the mean number of juveniles lost in nests with the mother present ($n = 11$, mean \pm SE = 1.73 ± 0.24) and those with no mother ($n = 26$, 1.77 ± 0.17) identified no significant differences between the two treatments ($F = 0.017$, NS): the presence of mothers appears to totally prevent predation from occurring as opposed to merely limiting the number of young lost.

DISCUSSION

Foreign spiders frequenting *A. studiosus* nests.—Censuses of *A. studiosus* populations across a broad portion of its latitudinal range indicate that foreign spiders commonly associate with *A. studiosus* nests. Salticids, anyphaenids, araneids, and tetragnathids were the numerically prominent nest associates across the latitudinal range studied, but agelenids and clubionids were also quite common. Although usually only one foreign spider was found in a host nest, when two or more individuals were present, they usually were not conspecifics, but rather belonged to families with dissimilar foraging strategies. One possible explanation for this observation is that nest associates of different familial affiliations might exploit different resources offered by the host nest compared to spiders that share a closer taxonomic affiliation. Another possibil-

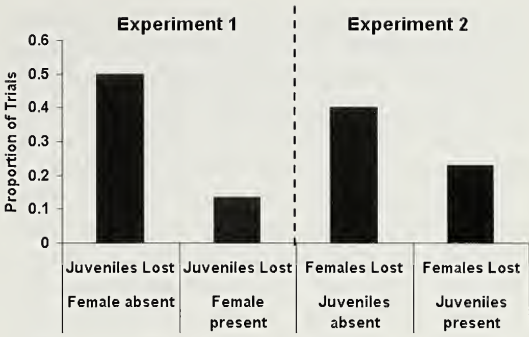


Figure 6.—Predation results for anti-predator trials: relationship between class present/absent and incidence of predation on other class.

ity is that because spiders have been shown to maintain energy-based territories throughout their lives and may even engage in territorial cannibalism (Riechert 1978, 1982; Marshall 1995; Moya-Laraño et al. 1996, 2002), spatial exclusion would be exhibited towards conspecifics.

We were most interested here in considering why foreign spiders were found associated with *A. studiosus* nests, as this might provide insight into whether their presence had costs or benefits to the host. The Anyphaenidae was the only spider family that significantly settled in the tubes that interconnected the choice chambers to one another as opposed to actually settling in the foliage or nests of *A. studiosus* (Fig. 2). The curvatures of the tubes provide an ideal location for the construction of the silk sac retreat members of this family build. The anyphaenids are a major problem to the gas grill industry, because they have an affinity for the burning tubes of these grills and block air flow through them causing explosions (Riechert, personal communication).

While the other foreign spider families chose to settle primarily in the chambers, they did not distinguish among chambers that offered a foliage cluster alone, one with a recently produced nest in the foliage cluster that lacked the host, and one that contained a foliage cluster with an occupied nest. The simplest explanation for this result is that foreign spiders simply chance upon *A. studiosus* nests and associate with them at particular sites because of generally high densities of the host and foreign species at the sites. Another alternative is that all of the choices we presented each test subject (foliage, silk web, host spi-

der) could cue the presence of *A. studiosus*. Riechert (1985) showed that when selecting web-sites in a laboratory experimental setup, the desert spider *Agelenopsis aperta* (Gertsch 1934) more often chose sites that were desirable in one respect and less than ideal in another, as opposed to choosing sites that were optimal with regard to both categories (temperature and prey in that case). This was despite the fact that the combined sites were equally as accessible as the suboptimal locations. One explanation Riechert offered for this result is that in multiple-goal contexts individuals will settle for choices that appear to be suboptimal because the optimum changes with increased search time (after Williams & Nichols 1984). Thus, accepting a suitable yet less than ideal opportunity is safer than risking either future unavailability of better resources (e.g., better nest sites are taken by conspecifics) or vulnerability associated with not making a choice at all (e.g., being eaten by a predator while searching for a nest site away from cover). Another possibility was that, in the desert environment, prey and temperature might be correlated: cuing on one or the other of these alternatives would have provided the same optimal result in nature.

Because the foreign spider test subjects we used in our choice trials were placed in a multiple-goal context, their indecision may not necessarily indicate a lack of preference for the alternatives we presented. Foliage clusters could cue the presence of *A. studiosus*. To test for correlated cues, we would need to complete additional choice tests in which the choice was among foliage and non-foliage containers with and without nests and host spiders. From the experiment we completed here, we can conclude only that the foreign spider taxa tested were not repelled by the presence of *A. studiosus* nests or spiders. Li & Jackson (1996), however, did find evidence of a spider web's repelling effect on other spiders. They completed two-chamber choice experiments on the araneophagic spider, *Portia fimbriata* Doleschal 1859 (Araneae, Salticidae), which preferred to attack spider lures in chambers lacking webs compared to those presented on webs.

Documenting costs vs. benefits.—The interaction trial results provided evidence that most interactions that might occur between *A. studiosus* and the spiders that associate with

its nests would be negative ones that incur a cost to the host. The Tetragnathidae were the only family tested that showed random positioning relative to *A. studiosus* in the arena to which pairs of spiders were released (i.e., 25% same corner, 50% adjacent corners, and 25% opposite corners). For the other families tested, the paired spiders settled significantly more often at opposite corners of the arena indicating repulsion or avoidance of one another. There was also a high incidence of predation by the foreign spiders on *A. studiosus* during the course of these trials. The anyphaenids and agelelids exhibited the majority of the predation events on *A. studiosus* in the experiment, despite the fact that most of the taxa that associated with *A. studiosus* nests were larger in size than this small theridiid. *Anelosimus* predated on only a couple of phidromids that were close in size to it and only on one larger spider, a salticid, during the course of the interaction trials.

The interaction trial results provided an upper limit estimate of the potential costs of foreign spider nest associates to *A. studiosus*. As there was no nest present in the trial, encounter between the foreign spider and *A. studiosus* was highly probable and escape from predation improbable. Nevertheless, results from the censusing of active nests over time at the 12 field sites support the findings of the interaction trials. The frequencies of the range of foreign spider taxa in host nests did not correlate with the rate of loss of nests at particular sites. However the rate of co-occurrence of *A. studiosus* with anyphaenids and agelelids (the two families that preyed significantly on the host in the interaction trials) was positively correlated ($R^2 = 71\%$) with the rate of *A. studiosus* nest extinction. Wise & Chen (1999), in a removal experiment, identified a similar example of intraguild predation in a forest floor arthropod community. Predation by two spider families, Ctenidae and Gnaphosidae, significantly depressed the population numbers of two *Schizocosa* species *S. ocreata* (Hentz 1844) and *S. stridulans* (Stratton 1984). Further study indicated that the noted araneophagic effects were complex and varied both spatially and temporally (Lensing & Wise 2004). An individual-based model of the *A. studiosus* system is under development that will address the population consequences of araneophagy to *A. studiosus*.

This modeling effort will have to include the significant levels of reciprocal protection from predation offered by mothers and juveniles, irrespective of age. Whether this implies the existence of an active defense mechanism remains uncertain. It appears more probable that the protection afforded by juveniles to the mother and the mother to juveniles is related to the quantity of silk present. From other work (Jones et al. 2007) we know that there is a significant correlation between the number of juveniles in a nest and nest volume. The silk network may well deter predators from locating the host spiders. Think of the silk in a nest as forming a maze; a predator might be millimeters away from its prey but on a different side of a silk wall. Many web-building spiders have structures called barrier webs attached to the capture web that function in this way and also alert the web owner to the presence of a potential predator. Inspection of the anti-predator trial data failed to support an alternative explanation for reciprocal protection—the idea that young are spared from predation in the presence of the mother and vice versa because the predator feeds on the type of individual we targeted as potential defender in the experiment. Under this latter scenario, for instance, juveniles might offer the mother protection from predation because the predator sates itself by feeding on them. We found no evidence for this type of benefit.

While the common spider inhabitants of social spider nests are kleptoparasites and facultative commensals (Buskirk 1981), this is not the case for *A. studiosus*. The nests and capture webs of this species are quite small compared to many social spider colonies. Most nests are single mother nests with the average number of females present in multiple female nests being three (Furey 1998; Jones et al. 2007). The nest structure, itself, does not provide space for commensals, which use the support strands as attachment points for their own webs. Rather, the spiders that associate with *A. studiosus* nests appear to be attracted to the foliage cluster the nests are built in and interactions between them and *A. studiosus* are either neutral or costly to the host species. We found no evidence for a particular foraging strategy (e.g., hunting, ambush, orb web) as having a common effect on *A. studiosus*. For instance, the two orb-weaving families that frequented the nests of *A.*

studiosus behaved differently to the host; the araneids were antagonistic, while the tetragnathids were indifferent to it. Other comparisons of this type could not be quantified because typically only one family within a foraging strategy was prominently represented in the nests of *A. studiosus*. As argued above for the lack of multiple conspecifics in the same host nest, within-guild competition for resources should be higher than between-guild competition.

The results of this study indicate that we can add anyphaenids (genus *Anyphaena*) and agelelids (genus *Agelemopsis*) to the salticids (Jackson 2000) and pholcids (Jackson & Rowe 1987) that engage in araneophagy in social spider nests. Although the salticids were the most common nest associates of *A. studiosus* in the nest censuses, the genera, *Hytia* and *Phidippus*, comprising the Salticidae in this system did not appear to be prominent predators on the host. Rather they may have utilized the nests as brooding sites; if a brood was present with a foreign spider in the collected nests, it usually belonged to a salticid. Perhaps the identification of an agelelid as being an araneophage is just as surprising as the failure of salticids to exhibit significant levels of araneophagy on *A. studiosus*. However, while members of the genus *Agelemopsis* occupy sheet webs with attached funnels, they are known to patrol the vegetation in the vicinity of the web and also predate on other spider taxa when encountered (Riechert 1991). There is evidence that the Anyphaenidae may be the foreign spider taxon that presents the most important consequences to the demographics of *A. studiosus* populations throughout its range. While the agelelids were prominent nest associates at some latitudes, anyphaenids were present at all latitudes and are even the common foreign spider found associated with *A. studiosus* nests in Uruguay (Viera et al. unpublished results). Foreign spider association with *A. studiosus* nests generally presents a potential fitness cost to *A. studiosus* and the anyphaenids clearly figure prominently in generating this cost.

ACKNOWLEDGMENTS

We wish to thank the Miccosukee Indian Tribe of Florida and the State Parks of Alabama, Florida, and Tennessee for permission to work on their lands. We also thank J. Ap-

podaca, S. Dalrymple, S. Duncan, and T.W. Perkins for help with data collection. This research was supported by the Office of the Chancellor and the Department of Ecology and Evolutionary Biology at the University of Tennessee and by grant # 0235311 from the Animal Behavior Program of the National Science Foundation.

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Manuscript received 14 July 2006, revised 14 February 2007.

TREBACOSA EUROPAEA, A NEW WOLF SPIDER FROM HUNGARY (ARANEAE, LYCOSIDAE)

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ABSTRACT. A new species of Lycosidae, *Trebacosa europaea*, is described from male specimens collected within reed beds of Lake Velencei from Hungary. The species represents the Palearctic sister species of the Nearctic *Trebacosa marxi* (Stone 1890), and occurs in a very specialized habitat of *Phragmites communis*.

Keywords: Palearctic sister species, lycosid spider, reed beds, scanning micrographs

During a faunal survey of reed beds within Hungary we found male specimens of a previously unnamed species of lycosid spider on the southern shore of Lake Velencei. The peculiar morphology of the spider suggested that it could not be placed in any genus currently known from Europe or Asia, and we eventually surmised that it belonged within the genus *Trebacosa* Dondale & Redner 1981. Although this genus was previously known from a single named species, *T. marxi* (Stone 1890), which is restricted to North America (Dondale & Redner 1981; Paquin & Dupérré 2003), there have been two recent reports of a species of *Trebacosa* from Europe. Villepoux (1995) reported the capture of a new species of this genus from France, and Zhukovets (2003) found a new species in Belarus. These two conference abstracts did not provide a description of either species. Dondale & Redner (1981) provided a detailed appraisal of the genus, and suggested that *Trebacosa* can be reliably distinguished from the very similar genus *Pirata* Sundevall 1833. The median apophysis of the male palp, which in males of *Pirata* is rather small and pointed, is massive and armed with two large, pointed processes in *Trebacosa* (Dondale & Redner 1981).

Although our reed bed survey only captured male specimens, we have decided to present a species description because we believe that the description will contribute to the knowledge on the species' European distribution and to the eventual discovery and description of female specimens.

MATERIAL AND METHODS

This study is primarily based on Barber pit-fall trappings that were carried out in the reed beds of Lake Velencei between November 2003 and June 2005. Traps consisted of 400 ml, 85 mm double cups, with 70% ethylene glycol used as preservative. We placed 28 traps in 7 rows, with 4 traps in each row amongst the coastline reeds. All specimens are deposited in the Soil Zoological Collection (former Arachnoidea Collection) of the Department of Zoology, Hungarian Natural History Museum (Budapest). The electron micrographs were prepared in the Hungarian Natural History Museum, Budapest (courtesy of Dr. Krisztina Buczkó) with a Hitachi SN 2600 scanning electron microscope. The drawings were made using a Leica MZ6 stereo microscope by Béla Kancsal. The new species was compared with specimens of *Trebacosa marxi*: 1 ♀, 1 ♂, CANADA, Ontario, Oliver Bog June, July 1987, D. Blades (det. J. Redner) (These two specimens are deposited in the collection of the first author (CSz = coll. Szinetár).) The following abbreviations were used in the manuscript: PME = posterior median eyes; AME = anterior median eyes; ALE = anterior lateral eyes. Measurements (mm) are expressed as means \pm SE.

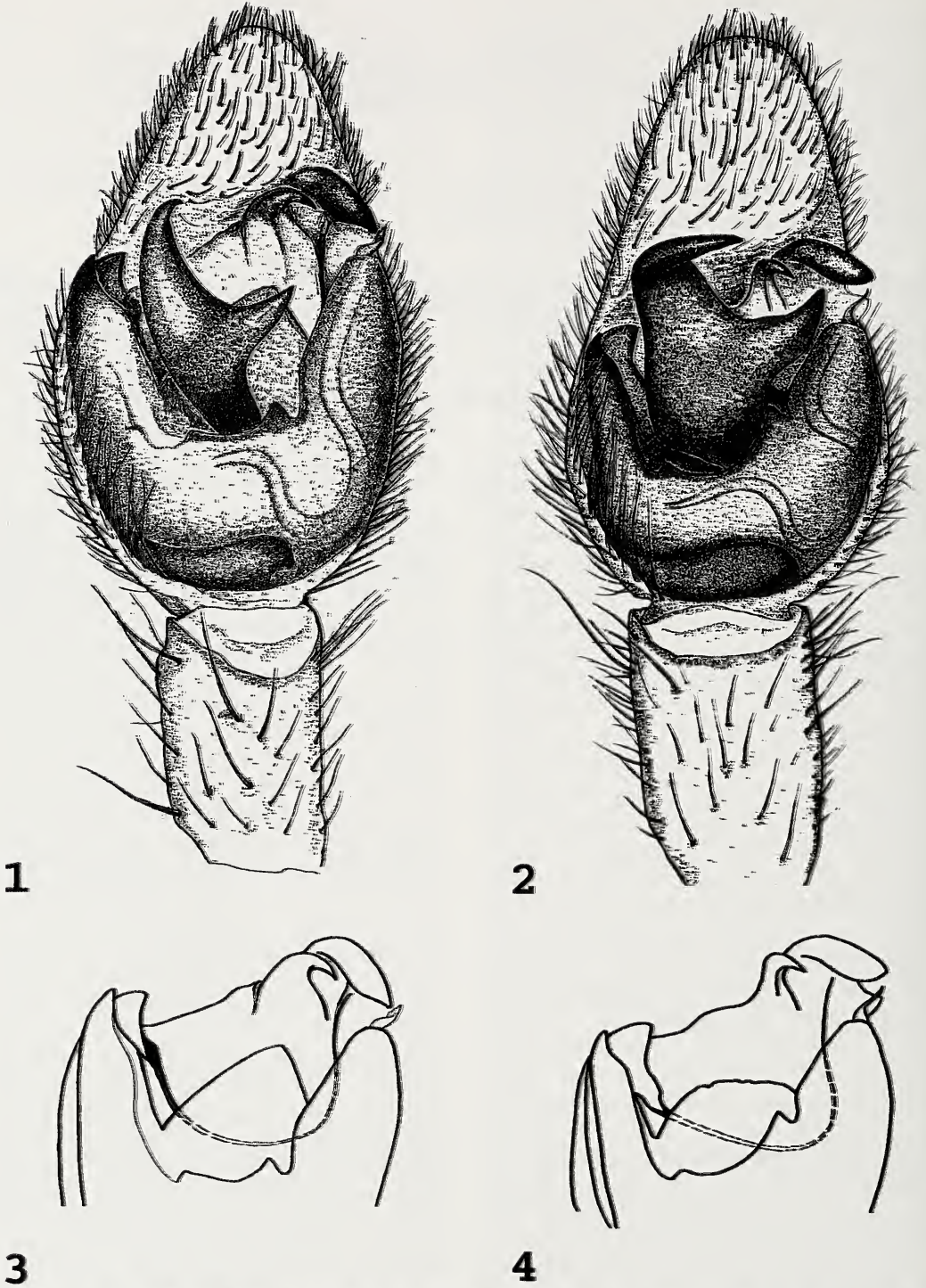
TAXONOMY

Family Lycosidae Sundevall 1833

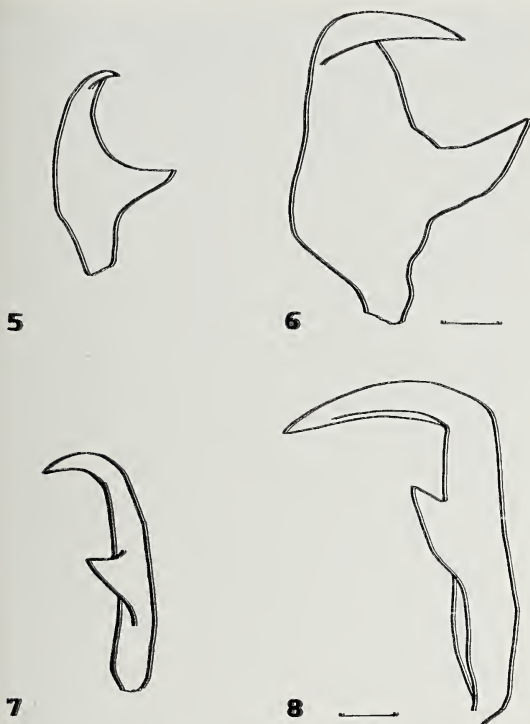
Genus *Trebacosa* Dondale & Redner 1981

Type species.—*Pirata marxi* Stone 1890, by original designation.

Remarks.—The only named species cur-



Figures 1-4.—Male palp of *Trebacosa* species: 1. Left palp of *T. europaea*, ventral view; 2. Left palp of *T. marxi*, ventral view; 3. Apical division of male genital bulb of *T. europaea*, ventral view; 4. Apical division of male genital bulb of *T. marxi*, ventral view.



Figures 5-8.—Median apophysis of the male palp of *Trebacosa* species: 5. *Trebacosa europaea*, ventral view; 6. *T. marxii*, ventral view; 7. *T. europaea*, lateral view; 8. *T. marxii*, lateral view. Scale line = 1 mm.

rently included in *Trebacosa* is *T. marxii* from North America (Dondale & Redner 1981; Paquin & Duperré 2003). The discovery of European species of *Trebacosa* (Villepoux 1995; Zhukovets 2003) expands the geographic distribution of the genus, and the description of a new species from Hungary presented here is only the second species of *Trebacosa* to be named.

Trebacosa europaea new species

Figs. 1, 3, 5, 7, 9, 11, 13

Material examined.—Holotype male: HUNGARY: *Mezőföld*: Lake Velencei Basin, István Chernel Bird Observatory (47°11'N, 18°36'E), Barber pitfall trap, 30 June 2004, Cs. Szinetár & B. Kancsal (HNHMB). Paratypes: 4 males, same location and collectors, 30 June 2004 (HNHMB); 10 males, same location and collectors, 25 July 2004 (HNHMB); 1 male, same location and collectors, 3 June 2005 (HNHMB).

Etymology.—The species name refers to

the currently known distribution of the species.

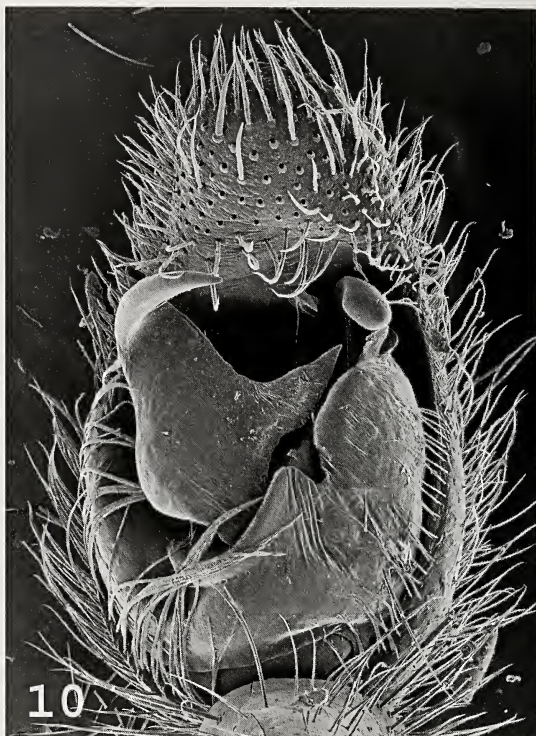
Diagnosis.—*Trebacosa europaea* can be distinguished from *T. marxii* as follows: the median apophysis (Figs. 5-8) is 1.2 times longer than broad in *T. marxii* and 1.7 times longer than broad in *T. europaea*, and the lower process of the median apophysis is similar to that in *T. marxii* but the upper process is shorter and more pointed. The upper branch of the terminal apophysis is clearly reflexed ventrally, while in *T. marxii* it is bluntly rounded (Figs. 13, 14). A central tegular process, which lies behind the median apophysis, is sub-triangular in *T. europaea* (Fig. 3) and rounded in *T. marxii* (Fig. 4). Also, the body dimensions of *T. europaea* are one-third smaller than those of *T. marxii*: *T. europaea* ($n = 10$): total length 4.75 ± 0.28 mm; carapace length 2.5 ± 0.16 mm; carapace width 1.6 ± 0.1 mm; and *T. marxii* (taken from Dondale & Redner 1981) ($n = 20$): total length 6.25 mm; carapace length 3.4 ± 0.32 mm; carapace width 1.6 ± 0.1 mm.

Description.—*Male*: Carapace dark orange. Three light-colored stripes in median line, fovea line and the line of posterior lateral eyes; the light median line is found along the entire carapace in some specimens, while the two lateral light stripes are limited to the pars cephalica. Fovea, radial stripes and carapaceal margin dark brown. Eye field slightly darker than remainder of carapace. PME row wider than frontal eye row. AME slightly larger than ALE.

Chelicerae: with 3 prolateral and 2 retrolateral teeth; color yellow-brownish, similar to color of sternum and leg coxae.

Abdomen: brown, bearing a lanceolate mark on anterior half of dorsum; blurred light-colored small spots form a pattern towards end of abdomen; posterior third of abdomen with a few darker transversal spots; ventral side lighter than dorsal side; color yellow-brownish, without any spots; spinnerets slightly darker than ventral side of abdomen; lighter color of ventral side continues upwards on side of abdomen and when viewed from above, forming a frame around dorsal pattern.

Legs: uniformly yellow orange. Setae ($n = 10$): femur I: dorsal 3, prolateral 0-1, retrolateral 0; tibia I: dorsal 0-1, prolateral 1-2, retrolateral 2, ventral 2p; basitarsus I: dorsal 0, prolateral 1-2, retrolateral 0-2, ventral 2p.



Figures 9, 10.—Scanning micrographs of the male palp, ventral view, of *Trebacosa* species: 9. *T. europaea*; 10. *T. marxi*.

Palp: median apophysis (Figs. 1, 9, 11) very large, 1.7 times longer than wide, and with two large pointed processes, each subequal in size (Figs 7, 11); upper process bent out only slightly towards terminal apophysis, and bent apically almost perpendicular to main axis of median apophysis (Figs. 1, 9); upper branch of terminal apophysis clearly bent basally (Fig. 13); central tegular process, which lies behind the median apophysis, subtriangular (Fig. 3); embolus long and slender, terminating near terminal apophysis; cymbium yellow orange; hairs not modified.

Somatic features ($n = 10$): total length: 4.75 ± 0.28 mm; carapace length: 2.5 ± 0.16 mm, carapace width: 1.6 ± 0.1 mm.

Female: Unknown.

Distribution.—Hungary.

Natural history.—The typical habitats of *T. marxi* are swamps, marshes, sphagnum bogs, and wet leaf litter (Dondale & Redner 1981), and our data demonstrate that *T. europaea* occurs in similar wetland habitats. The two previous reports of *Trebacosa* in Europe also mentioned similar habitats (Villepoux 1995; Zhukovets 2003). Specimens of *T. eu-*

ropaea were collected in a reed bed on the southern shore of Lake Velencei. The dominant species of the shoreline association (*Phragmitetum communis*) is *Phragmites australis*. Further species include *Typha angustifolia*, *Eupatorium cannabinum*, *Calystegia sepium*, *Solanum dulcamara*, *Echinocystis lobata*, *Lycopus europaeus* and *Mentha arvensis*. The specimens were captured 5–15 m from the open water surface. The soil water in this zone is very close (2–5 cm) to the soil surface and the decaying plant material and mosses are continuously soaked with water.

We collected and identified 3,922 specimens of 89 ground-dwelling spider species from reed beds between November 2003 and June 2005. Several species were found that are rare, habitat specialist spiders of European reed beds, indicating the natural value of the area. Some interesting spider species that co-occurred with *Trebacosa europaea* included: *Ero cambridgei* (Kulczyński 1911); *Crustulina sticta* (O. Pickard-Cambridge 1861); *Aracaeoncus crassipes* (Westring 1861); *Entelecara omissa* (O. Pickard-Cambridge 1902); *Glyphesis servulus* (Simon 1881); *G. taople-*



Figures 11–14.—Scanning micrographs of apophyses in male palps of *Trebacosa* species: 11. Median apophysis of *T. europaea*, lateral view; 12. Median apophysis of *T. marxi*, lateral view; 13. Terminal apophysis of *T. europaea*, lateral view; 14. Terminal apophysis of *T. marxi*, lateral view.

sius Wunderlich 1969; *Pelecopsis mengei* (Simon 1884); *Walckenaeria unicornis* (O. Pickard-Cambridge 1861); *Pirata tenuitarsis* (Simon 1876); and *Argyroneta aquatica* (Clerck 1757).

The majority of the dominant spider species were tolerant, commonly occurring, ground-dwelling species: *Alopecosa pulverulenta* (Clerck 1757); *Pardosa prativaga* (L. Koch 1870); *Trochosa ruricola* (De Geer 1778); *Antistea elegans* (Blackwall 1841); *Agracina striata* (Kulczyński 1882); *Drassyllus lutitanus* (L. Koch, 1866); *Trachyzelotes pedestris* (C.L. Koch 1837). Rare orb-weaver species,

such as *Larinia elegans* Spassky 1939 and *L. bonneti* Spassky 1939 were also found (Szinetár & Eichardt 2004). The male specimens of *T. europaea* were collected from May to July, which is likely to represent the main activity period of both sexes. However, we do not have data on females.

Biogeography.—The discovery of European species of *Trebacosa* (Villepoux 1995; Zhukovets 2003) has shown that the genus is present in both the Nearctic and Palearctic regions and, if all European populations are eventually found to be conspecific, *T. marxi* in North America and *T. europaea* in Europe

may be postulated as sister species. Formation of the genus presumably took place by the end of the Lower Eocene when North America had direct land connection with Europe via Greenland and Scandinavia (Cox et al. 1973).

The discovery of a previously unnamed, medium-sized spider in central Europe is surprising, especially as *T. marxi* was first described over 100 years ago, but the highly specialized habitat in which *T. europaea* was found has been less intensively studied than other terrestrial habitats in Europe. This claim is also supported by recent discoveries of several water-bound species from Central Europe (e.g., Uhl et al. 1992; Szinetár & Eichardt 2004).

ACKNOWLEDGMENTS

The authors are grateful to Dr. C.D. Dondale for donating *T. marxi* specimens, to Nadine Dupérré for her assistance in acquiring literature. We are grateful to Krisztina Buczkó and Tamás Szűts for their help with the scanning micrographs. The authors wish to thank Mr. Péter Ujhelyi, Warden of the Chernel István Bird Observatory, to Mr. Ferenc Falussy, Director of the Inspectorate of Lake Velencei, and to the Directorate of the Duna-Ipoly National Park for their kind permission to carry out the survey. Csaba Szinetár was supported by a Bolyai Fellowship of the Hungarian Academy of Sciences. Sz. Lengyel improved the English text. Special thanks to two referees for their critical reviews of a draft of this paper.

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Manuscript received 5 May 2006, revised 13 July 2006.

REVISION OF THE NEOTROPICAL SPIDER GENUS *MACRINUS* (ARANEAE, SPARASSIDAE)

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ABSTRACT. The sparassid genus *Macrinus* Simon 1887 is revised, the type species, *M. succineus* Simon 1887, is redescribed and *Olios pollexensis* Schenkel 1953 is transferred to the genus. Females are described and illustrated for the first time. *Macrinus milleri* Caporiacco 1955 is placed as *incertae sedis* and a new species, *Macrinus jaegeri*, is described from the states of Pará and Mato Grosso, Brazil.

Keywords: Taxonomy, new species, South America

The taxonomic history of the genus *Macrinus* Simon 1887 is somewhat confusing. The genus was originally proposed by Simon (1887) to include three Brazilian species: the type species *Macrinus succineus* Simon 1887 from São Paulo de Olivença and *M. longipes* Simon 1887 from Fonte Boa, both in the state of Amazonas, and *M. atomarius* Simon 1887 from Rio de Janeiro, Rio de Janeiro.

Ten years later, Simon (1897) stated that although he placed *M. succineus* in a separate genus he could not be sure that this species is not congeneric with those of the genus *Sparassus* Walckenaer 1805. He transferred the species to *Sparassus* but said nothing whatsoever about the remaining *M. longipes* and *M. atomarius*. Later, in 1911, Petrunkevitch transferred *M. succineus* to *Olios* Walckenaer 1837 and formally synonymized both genera. In addition he proposed the new name *attractus* for *Olios atomarius*, preoccupied by Simon (1880). Years later, Roewer (1951) proposed the new name *longipeditus* for *M. longipes*, preoccupied by Walckenaer (1837).

In 1955, *Macrinus* was implicitly revalidated by Caporiacco, who described *Macrinus milleri* Caporiacco 1955, based on a male from Rancho Grande, Aragua, Venezuela. Once again, nothing was said about either *O. longipeditus* (*M. longipes*) or *O. attractus* (*M. atomarius*), which to date, remain in the genus *Olios*. Although these species are clearly not congeneric with the type species of *Olios*, *O. argelasius* (Walckenaer 1805), they cannot, at present, be placed in any other known genus

of Sparassidae. Thus, until the present study, the genus *Macrinus* was composed of only two species, *M. succineus* and *M. milleri*, both known only from males.

In this study, a revision of the genus *Macrinus* is presented. The type species, *M. succineus*, is redescribed and *Olios pollexensis* Schenkel 1953 is transferred to the genus. Their females are described and illustrated for the first time. In addition, a new species is described from Pará and Mato Grosso, Brazil. *Macrinus milleri* is found not to be congeneric with the type species, *M. succineus*, and, thus, is placed as *incertae sedis* until further knowledge on the Neotropical Sparassidae fauna is attained.

METHODS

The material examined belongs to the following institutions (Abbreviation and curator in parenthesis): American Museum of Natural History, New York (AMNH, N.I. Platnick); Instituto Butantan, São Paulo (IBSP, A.D. Brescovit); Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre (MCN, E.H. Buckup); Museu de Ciência e Tecnologia da PUC/RS, Porto Alegre (MCTP, A.A. Lise); Museu Nacional do Rio de Janeiro, Rio de Janeiro (MNRJ, A.B. Kury); Museo de la Universidad Central de Caracas, Caracas (MUCV, R. Cândia); Museu de Zoologia da Universidade de São Paulo, São Paulo (MZSP, R. Pinto da Rocha); Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe (SMNK, H. Höfer); Muséum Na-

tional d'Histoire Naturelle, Paris (MNHN, C. Rollard); Naturhistorisches Museum Basel, Basel (NHMB, U. Wüest); Museum of Natural History, Smithsonian Institution, Washington DC (USNM, J.A. Coddington).

Abbreviations used throughout the text are: ALE = anterior lateral eyes; ALS = anterior lateral spinnerets; AME = anterior median eyes; d = dorsal; p = prolateral; PLE = posterior lateral eyes; PLS = posterior lateral spinnerets; PME = posterior median eyes; PMS = posterior median spinnerets; r = retrolateral; v = ventral. Measurements are in mm. Epigyna were dissected and submerged in clove oil to study internal structures. Micrographs were obtained with a JEOL (JSM 840A) scanning electron microscope from the "Laboratório de Microscopia Eletrônica do Departamento de Física Geral do Instituto de Física da Universidade de São Paulo (USP)".

TAXONOMY

Family Sparassidae Bertkau 1872

Genus *Macrinus* Simon 1887

Macrinus Simon 1887:470; Caporiacco 1955:404; Platnick 2006.

Sparassus Walckenaer 1805: Simon 1897:37 (in part)

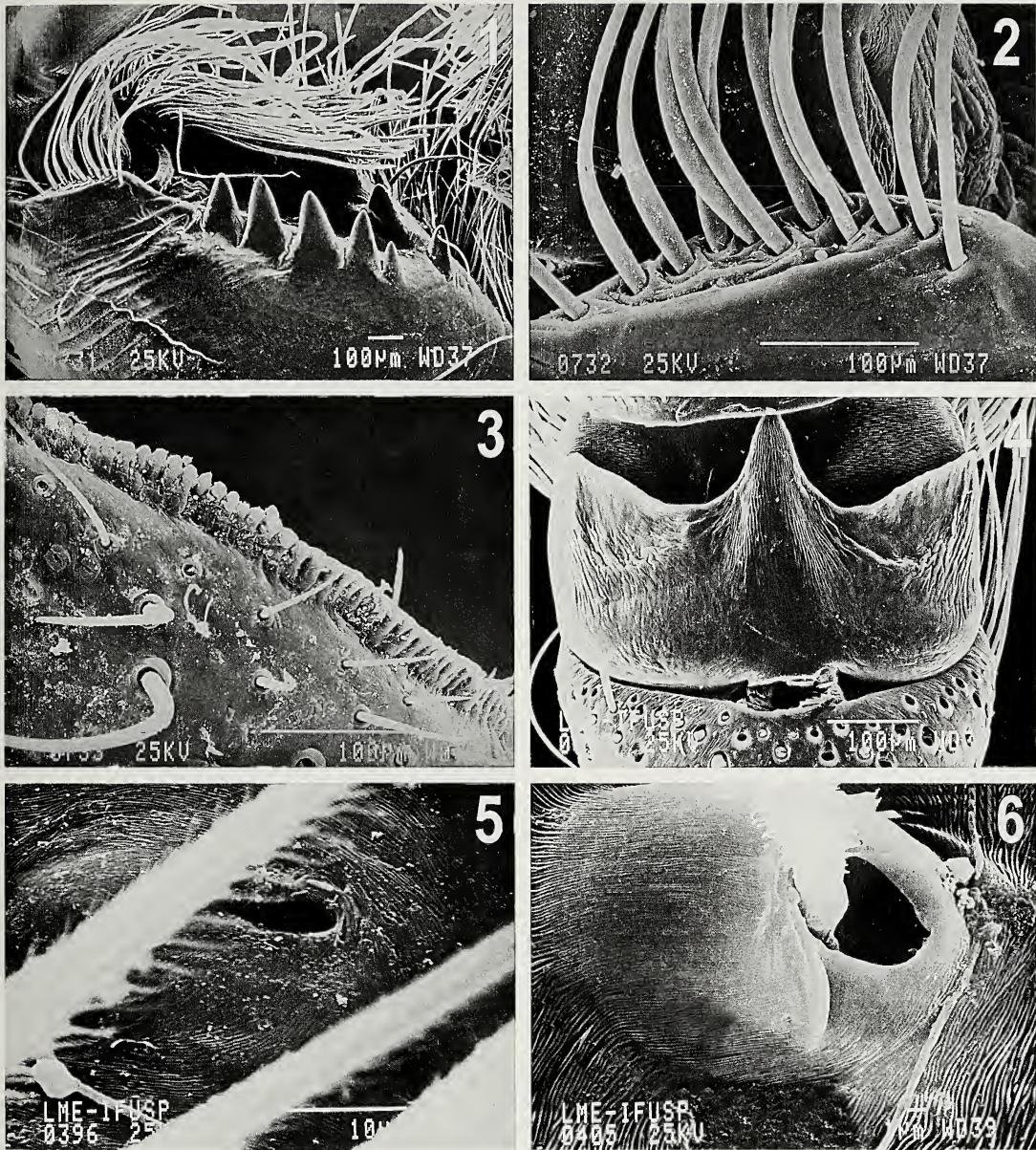
Olios Walckenaer 1837: Petrunkevitch 1911:503 (in part).

Type species.—*Macrinus succineus* Simon 1887 by original designation.

Diagnosis.—Species included in the genus *Macrinus* are distinguished from the remaining Sparassidae by the twisted tegulum (Figs. 22, 28, 34) with distal prolateral laminar projection (LP, Figs. 23, 29, 35) and a fulcrum (F) with a prolateral dorsal serrated projection (SP) (Figs. 17, 18, 21, 27, 33) on the male palp. Females are distinguished by the rounded lateral lobes (LL) that partially cover the median septum (MS) in the female epigynum (Figs. 24, 30, 36), by the spermathecae with a hyaline sac-like head (SH) and a small base (SB) (Figs. 25, 31, 37) and by the general course of the internal duct system (Figs. 26, 32, 38).

Description.—Total length (males and females) 10.1–22.3. Prosoma slightly longer than wide (Fig. 19); cephalic region slightly higher than thoracic region, gradually flattening posteriorly. Fovea conspicuous on poste-

rior third of prosoma. Eyes arranged in two rows, the anterior very slightly recurved or straight; AME larger than ALE and more distant from each other than from laterals. Posterior eye row straight; PME smaller than PLE and slightly more distant from each other than from laterals (Fig. 19). Clypeus low, less than AME diameter. Chelicerae longer than wide. Cheliceral groove with two promarginal teeth, the basal smaller, and five retromarginal teeth, four subequal and a smaller basal one. Inter-marginal denticles absent (Fig. 1). Internal keel with 10–12 strong setae, arranged in an irregular row (Figs. 1, 2). Labium rebordered, slightly wider than long. Endites slightly convergent, longer than wide with a dense scopulae in internal margin. The outer margin slightly concave (Fig. 20). Serrula with a single row of denticles (Fig. 3). Sternum as long as wide, slightly projected between coxae IV (Fig. 20). Legs laterigrade (2143). Leg spination in males: femora I–III: d0-1-1; p1-1-1; r1-1-1; femur IV: d0-1-1; p1-1-1; r0-0-1; tibiae I–II: d1-0-1; p1-0-1; r1-0-1; v2-2-0; tibiae III–IV: d0-0-1; p1-0-1; r1-0-1; v2-2-0; metatarsi I–III: p1-1-0; r1-1-0; v2-2-0; metatarsi IV: p1-1-1; r1-1-1; v2-2-0. Leg spination in females as in males, except tibiae I–IV: d0. Metatarsi I–IV with trilobate membrane with median hook slightly more developed than laterals (Fig. 4). Tarsi and anterior half of metatarsi scopulate. Tarsal organ capsulate with oval opening, located dorsally at the distal end of tarsi (Fig. 5). Trichobothria present on dorsal tibiae metatarsi and tarsi, arranged in two parallel rows that converge to a single file on posterior half of tarsi and on metatarsi. Bothrium with crescent plate, with few transversal distal grooves, projected over a smooth basal plate (Fig. 6). Tarsi with pair of pectinate claws, with 25–30 teeth, and claw tufts (Fig. 7). Female pedipalp with a single pectinate claw (Fig. 8). Opisthosoma oval, longer than wide. Six spinnerets: ALS contiguous, conical and bi-segmented. Basal segment slightly elongate and cylindrical. Distal segment short and truncated with a pair of major ampullate gland spigots and several piriform gland spigots (Figs. 9, 10); AMS conical and short with pair of minor ampullate gland spigots, 2–4 cylindrical gland spigots and 20–25 aciniform gland spigots (Fig. 11); PLS conical and bi-segmented. Basal segment slightly elongate

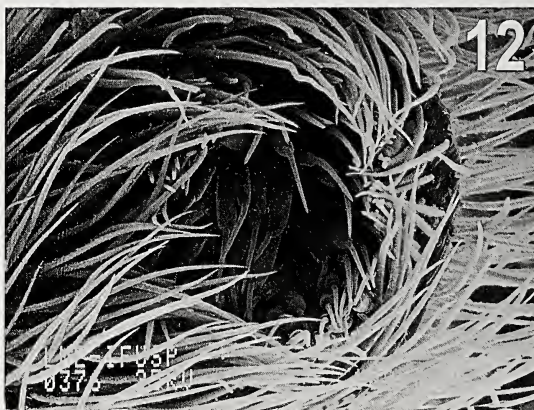
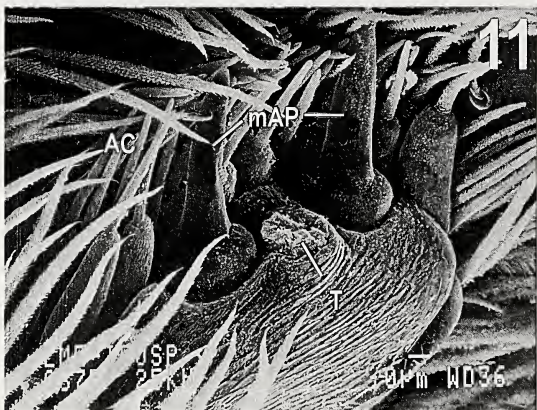
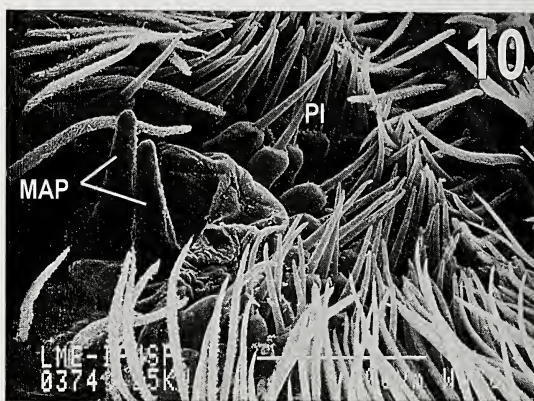
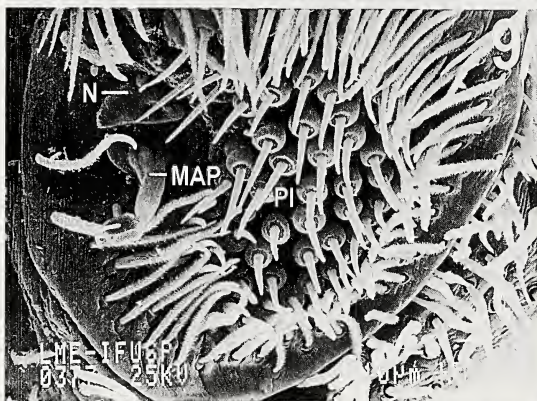
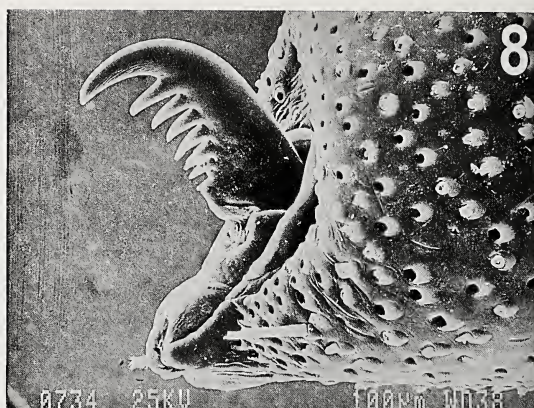
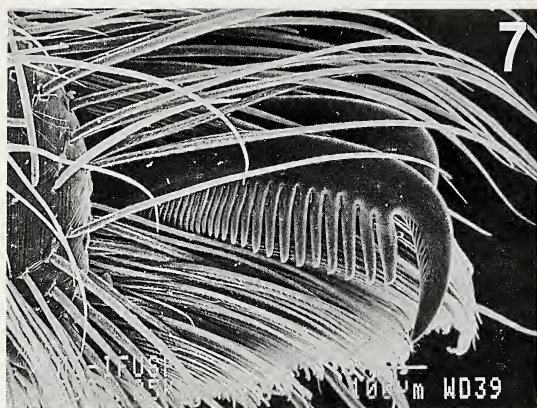


Figures 1–6.—*Macrinus succineus* Simon, male: 1. Right chelicerae, dentition; 2. Keel at base of fang, detail of setae; 3. Left endite, serrula; 4. Metatarsus I, trilobate membrane; 5. Tarsus I, tarsal organ; 6. Tarsus I, base of trichobothria.

and cylindrical. Distal segment short and truncated with many aciniform gland spigots (Fig. 12).

Palp: Tibia slightly elongate with one short retrolateral and one long prolateral spine at the base (Figs. 22, 28, 34). RTA short, distally curved and tapered with a slightly swollen area at the base (Figs. 13, 14, 22, 28, 34). Cymbium elongate, covered with short slen-

der hairs, with oval alveolus. Tegulum twisted (Figs. 22, 28, 34); retrolaterally with either a spiny field (Figs. 15, 23, 29) or a short projection (Figs. 16, 34); distally with a retrolateral laminar projection that partly supports the median section of the embolus (Figs. 23, 29, 35) and a prolateral fulcrum with a dorsal serrated projection (Figs. 21, 27, 33). Embolus long and filiform, anteriorly curved back-



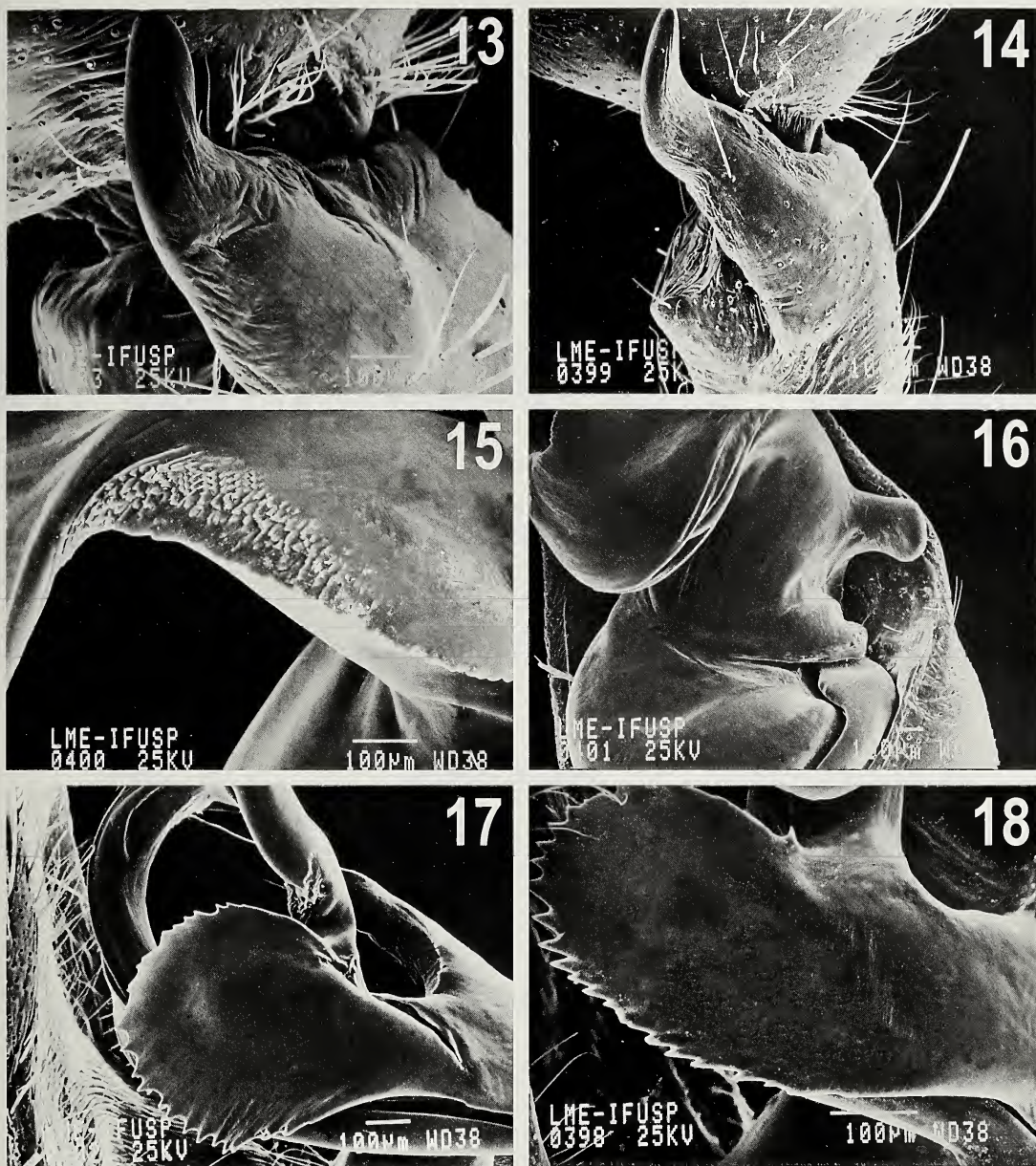
Figures 7–12.—*Macrinus succineus* Simon: 7. Male, tarsus I, claws; 8. Female, pedipalp, claw; 9. Male, ALS; 10. Female, ALS; 11. Male, PMS; 12. PLS (AC = aciniform gland spigots; MAP = major ampullate gland spigots; mAP = minor ampullate gland spigots; N = nubin; PI = piriform gland spigots; T = tartipore; TO = tarsal organ).

wards and resting, posteriorly, in the fulcrum (Figs. 17, 18, 22, 28, 34).

Epigynum: Epigynal field with pair of rounded lateral lobes slightly covering the median septum and a pair of copulatory openings (CO, Figs. 24, 30, 36). Vulva with copulatory duct (CD) long and U-shaped. Spermathecae

head (SH) hyaline and sac-like, connected to small, slightly elongate base (SB) by a long and narrow stalk. Fertilization ducts (FD) short and curved (Figs. 25, 26, 31, 32, 37, 38).

Distribution.—Neotropical. Known from South America, from southeastern Brazil to Venezuela.



Figures 13–18.—13. *Macrinus succineus* Simon, male, left palp, RTA; 14. *Macrinus pollexensis* (Schenkel), male, left palp, RTA; 15. *M. succineus*, left palp, tegulum, retrolateral spiny field; 16. *M. jaegeri* new species, left palp, tegulum, retrolateral projection; 17. *M. succineus*, left palp, serrated projection at base of the embolus; 18. *M. pollexensis*, left palp, serrated projection at base of the embolus.

Composition.—*Macrinus succineus* Simon, *Macrinus pollexensis* (Schenkel) new combination, *Macrinus jaegeri* new species.

Insertae sedis.—*Macrinus milleri* Caporiacco 1955:404, figs. 57a–b (Male holotype from Rancho Grande, Aragua, Venezuela, deposited in MUCV 810, examined); Platnick 2006.

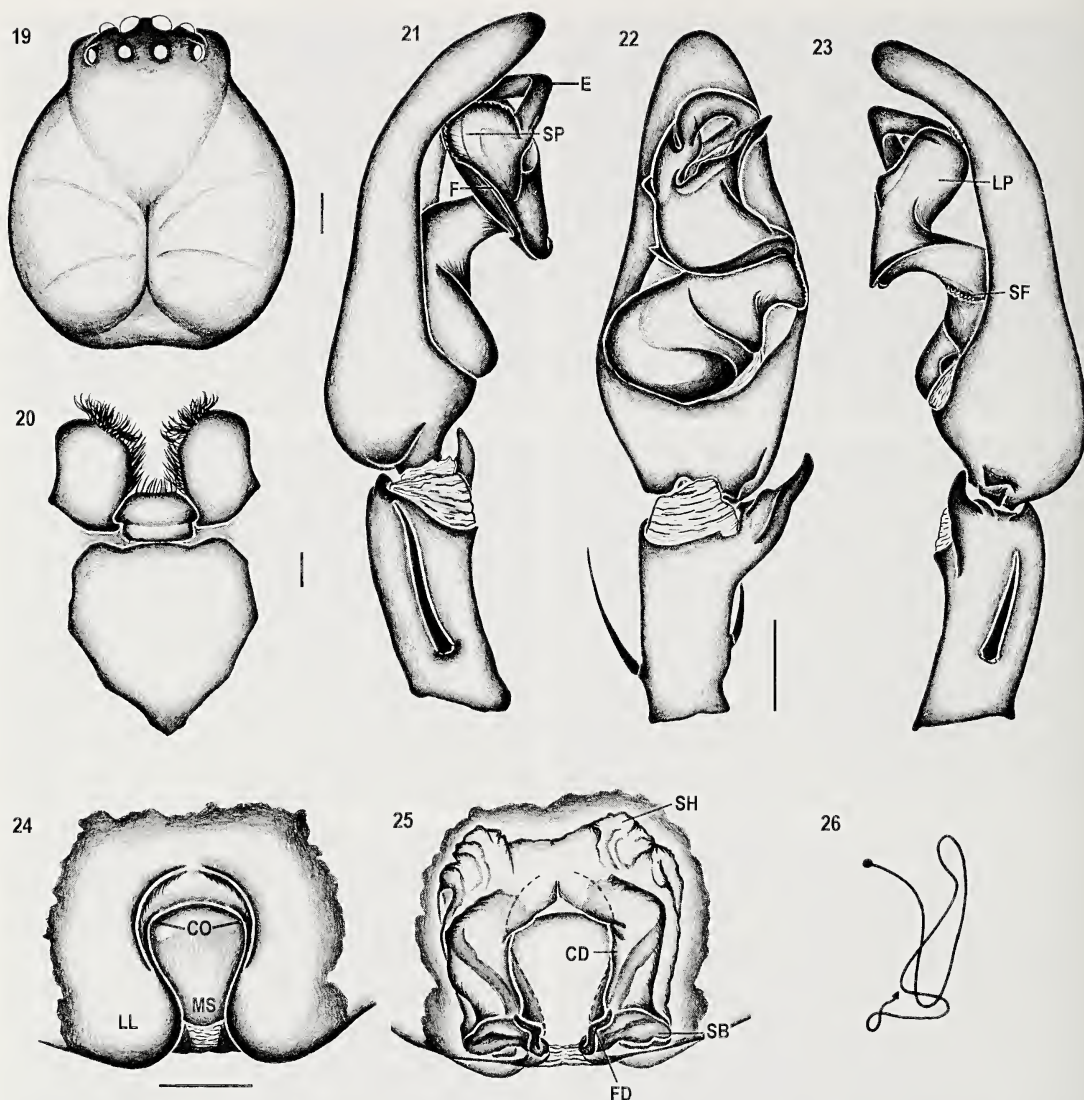
Macrinus succineus Simon 1887

Figs. 1–13, 17, 19–26

Macrinus succineus Simon 1887:470; Platnick 2006.

Sparassus succineus: Simon 1897:46.

Olios succineus: Petrunkevitch 1911:503; Roewer 1954:709; Bonnet 1958:3181.

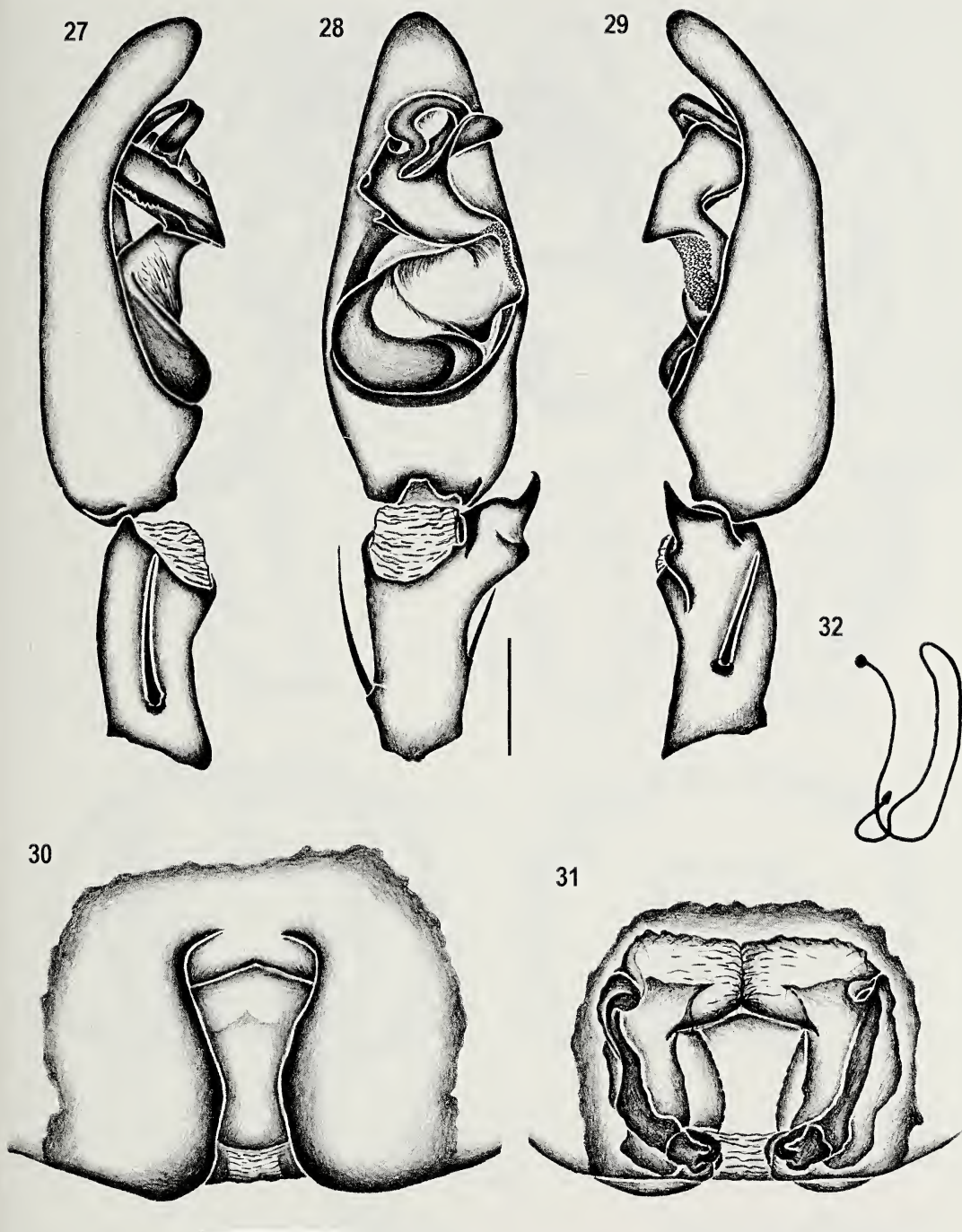


Figures 19–26.—*Macrinus succineus* Simon: 19. Male, prosoma, dorsal view; 20. Labium, endites and sternum, ventral view; 21. Left palp, prolateral view; 22. Ventral view; 23. Retrolateral view; 24. Female, epigynum, ventral view; 25. Vulva, dorsal view; 26. General course of internal duct system (CD = copulatory duct; CO = copulatory opening; E = embolus; F = fulcrum; FD = fertilization duct; LL = lateral lobes; LP = laminar projection; MS = median septum; SB = spermathecae base; SF = spiny field; SH = spermathecae head; SP = serrated projection). Scale lines = 1.00 mm.

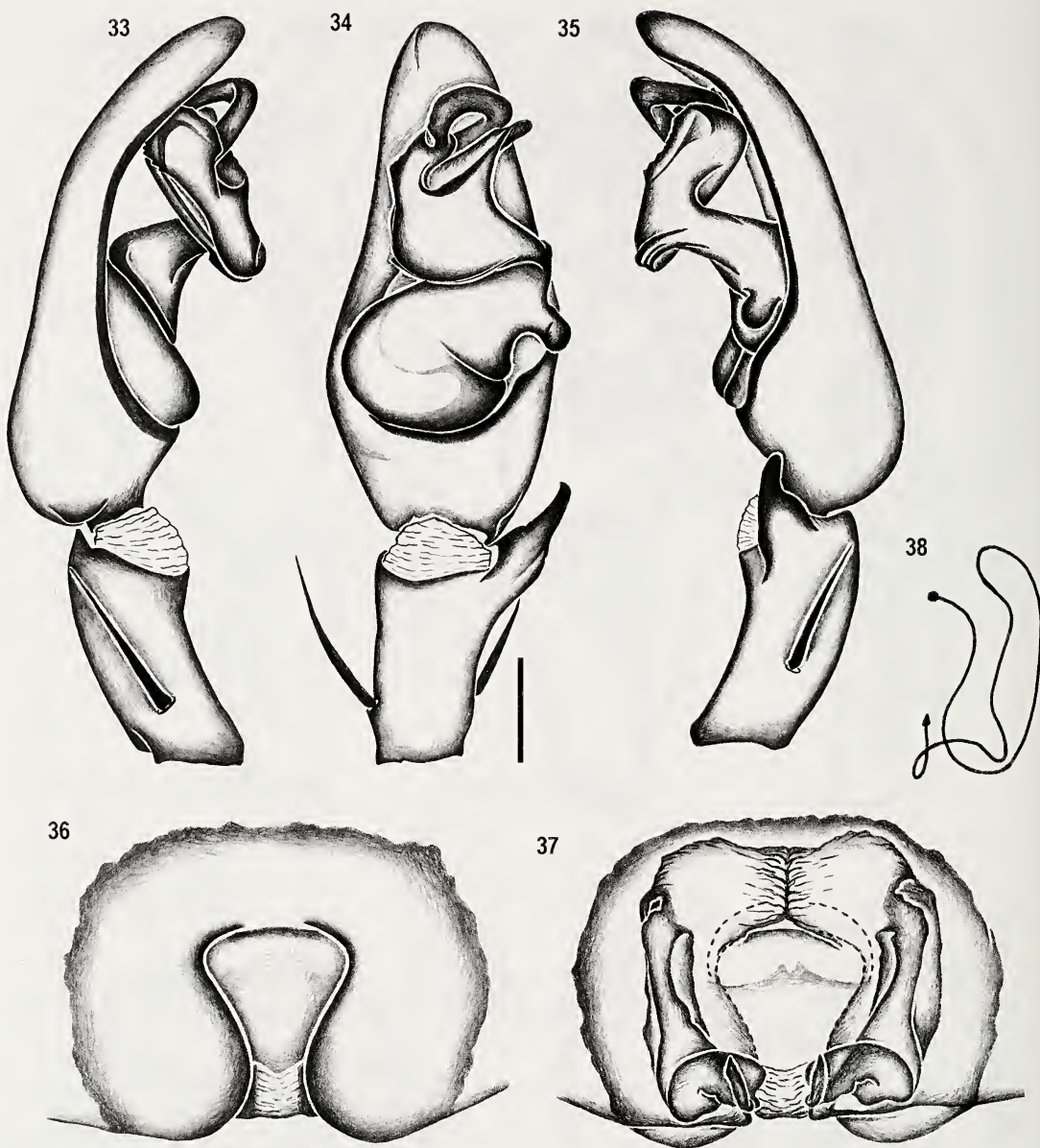
Type specimen.—Holotype male, São Paulo de Olivença, Amazonas, Brazil (03°27'S, 68°47'W) (MNHN 7316), examined

Other material examined.—SURINAME: *Marowijne*: 1 ♂, Anapaike Village, Lawa River (05°42'N, 54°00'W), 1 ♀, 8–29 November 1963, B. Malkin (AMNH). ECUADOR: *Francisco de Orellana*: Reserva Etnica de Waorani, 1 km S. Onkone Gare Camp (00°39'25.7"S, 76°27'10.8"W), 10 October

1994, T.L. Erwin et al. (USNM). BRAZIL: *Amazonas*: 2 ♂, Presidente Figueiredo, Usina Hidrelétrica de Balbina (02°02'S, 60°02'W), 1987–1988, Equipe IBSP (IBSP 7347; 7344); 1 ♂, Manaus, Igapó Tarumã-Mirim (03°06'S, 60°01'W), 8 December 1976, H. Höfer (SMNK); 1 ♀, same data except 10 November 1976 (SMNK); 1 ♀, same data except 14 February 1983 (SMNK); *Acre*: 1 ♀, Rio Branco (07°31'S, 73°01'W), 6 November 1995, E.P.



Figures 27–32.—*Macrinus pollexensis* (Schenkel): 27. Male, left palp, prolateral view; 28. Ventral view; 29. Retrolateral view; 30. Female, epigynum, ventral view; 31. Vulva, dorsal view; 32. General path of internal duct system. Scale lines = 1.00 mm.



Figures 33–38.—*Macrinus jaegeri* new species: 33. Male, left palp, prolateral view; 34. Ventral view; 35. Retrolateral view; 36. Female, epigynum, ventral view; 37. Vulva, dorsal view; 38. General course of internal duct system. Scale lines = 1.00 mm.

Ferreira (IBSP 7008); *São Paulo*: 1 ♂, 1 juvenile, Campinas, Fazenda Rio das Pedras (22°53'S, 47°04'W), 9 May 1974, C.R. Bertim et al. (IBSP 26794); 1 ♂, Primavera, Usina Hidrelétrica Engenheiro Sérgio Motta (21°58'S, 49°58'W), January–February 2000, Equipe IBSP (IBSP 29979); *Mato Grosso do Sul*: 1 ♂, 1 ♀, Anaurilândia, Usina Hidrelétrica Engenheiro Sérgio Motta (22°22'59"S,

52°48'42.4"W), 15 November–23 December 1998, Equipe IBSP (IBSP 23492, 23356). *BO-LÍVIA*: 1 ♂, no further data (AMNH); *Beni*: 27 km SW of Yucumoca (15°23'S, 66°59'W), 15–19 November 1989, Coddington, Griswold, Silva, Larcher & Penaranda (USNM); *Santa Cruz*: San Ignacio (14°49'S, 61°28'W), 9 March 1961, L. Hammerschmidt (IBSP 3809).



Figure 39.—Map of South America showing known distributions of species of *Macrinus*.

Diagnosis.—Males of *Macrinus succineus* resemble those of *M. pollexensis* by the presence of a retrolateral spiny field (Fig. 15) in the tegulum of the palp. They are distinguished by the smoothly curved RTA (Figs. 13, 23), by the wider distal part of the tegulum (Fig. 22) and by the wider serrated projection at the base of the embolus of the male palp (Figs. 17, 21). Females are distinguished from the remaining *Macrinus* by the distally rounded median septum of the epigynum (Fig. 24) and by the small and rounded base of the spermathecae (Fig. 25).

Description.—*Male* (IBSP 7347): prosoma orange, slightly darker at eye area; fovea dark brown; clypeus brown; chelicerae dark orange with brown internal margins; legs and pedipalps orange; sternum orange with darker margins; labium dark orange, distally cream colored; endites orange, distally cream colored; opisthosoma yellow to pale orange. Total length 15.6. Prosoma: 7.1 long, 6.2 wide. Eye diameters and interdistances: AME 0.5, ALE 0.34, PME 0.3, PLE 0.4, AME–AME 0.2, AME–ALE 0.04, PME–PME 0.54, PME–PLE 0.32, AME–PME 0.36, ALE–PLE 0.3. Leg measurements: leg I: femur 11.5, patella 4.0, tibia 11.8, metatarsus 13.0, tarsus 3.2, total 43.5; leg II: femur 12.2, patella 4.0, tibia 12.3, metatarsus 14.3, tarsus 3.2, total 46.0; leg III: femur 10.2, patella 3.5, tibia 9.3, metatarsus 9.7, tarsus 2.5, total 35.2; leg IV: femur 11.0, patella 3.5, tibia 9.6, metatarsus 11.4, tarsus 3.0, total 38.5. Leg spination follows generic pattern. Palp: tegulum twisted with a retrolateral spiny field (Fig. 23) and wide and rounded serrated laminar projection at the base of the embolus (Figs. 17, 21). Opisthosoma oval: 8.0 long, 6.0 wide.

Female (IBSP 7363): Coloration as in male. Total length 20.2. Prosoma: 7.5 long, 6.9 wide. Eye diameters and interdistances: AME 0.44, ALE 0.4, PME 0.28, PLE 0.3, AME–AME 0.3, AME–ALE 0.14, PME–PME 0.56, PME–PLE 0.6, AME–PME 0.4, ALE–PLE 0.36. Leg measurements: leg I: femur 9.5, patella 3.7, tibia 8.7, metatarsus 9.2, tarsus 2.5, total 33.6; leg II: femur 10.0, patella 3.6, tibia 9.1, metatarsus 9.2, tarsus 2.5, total 34.4; leg III: femur 8.7, patella 3.2, tibia 6.7, metatarsus 6.6, tarsus 1.9, total 27.1; leg IV: femur 9.2, patella 3.1, tibia 7.5, metatarsus 8.1, tarsus 2.0, total 29.9. Leg spination follows generic pattern. Opisthosoma oval: 11.6 long, 7.6

wide. Epigynum with anteriorly rounded median septum (Figs. 24).

Variation.—Seven males: total length 13.6–15.6; prosoma length 5.6–7.2; femur I 9.5–12.0. Five females: total length 16.3–20.2; prosoma length 6.3–7.6; femur I 8.9–9.9.

Distribution.—Known from Bolívia, oriental Amazonia, southeastern and central Brazil

Macrinus pollexensis (Schenkel 1953)
new combination

Figs. 14–15, 18, 27–32

Olios pollexensis Schenkel 1953:41, fig. 35; Brignoli 1983:595; Platnick 2006.

Type specimen.—Holotype male, El Pozon, Fálcon, Venezuela (12°05'N, 69°59'W) (NHMB 2262-a), examined.

Other material examined.—VENEZUELA: *Distrito Federal*: 1 ♀, Caracas, El Valle (10°30'N, 66°55'W), 28 March 1939, G. Vivas Berthien (MNRJ 1738); *Bolívar*: 1 ♀, Salto Angel (Parque Nacional Canaima) (05°31'N, 61°56'W), 7 November 2001, M.O. Gonzaga (IBSP 34839); BRAZIL: *Amazonas*: 1 ♂, Manaus (Igapó Tarumã-Mirim) (03°06'S, 60°01'W), 25 November 1976, H. Höfer (SMNK); 1 ♂, (Reserva Florestal Adolpho Ducke) (03°06'S, 60°01'W), 23 September 1991, H. Höfer, T. Gasnier (SMNK 3636); 1 ♂, same location, 1 June 1992, T.R. Gasnier (MCN 22242); 1 ♀, 1 juvenile, (Rio Negro) (03°06'S, 60°01'W), no date, no collector (MNRJ 13099); *Pará*: 1 ♂, Belém (01°26'S, 48°28'W), 15 November 1951, P. Ledoux (IBSP 556); *Maranhão*: 1 ♂, Balsas, Gerais de Balsas (Tem Medo River margin) (07°31'S, 46°01'W), 8 November 1999, Dietz & Yamamoto (MZSP 20606); *Paraíba*: 1 ♂, João Pessoa (Campus II da Universidade Federal da Paraíba) (07°07'S, 34°52'W), 28 May 2003, S.C. Dias (IBSP 41001); *Pernambuco*: 1 ♀, Tapera (currently Bonança), Moreno (08°24'S, 38°04'W), B. Pickel (MNRJ 1739); *Sergipe*: 1 ♀, Santa Luzia do Itanhi (Mata do Crasto, 11°23'S, 37°24'W), 9–13 September 1999, A.D. Brescovit et al. (IBSP 43270); *Bahia*: 1 ♂, Itamarajú (17°04'S, 39°31'W), no date, no collector (MNRJ); 1 ♂, (Fazenda Pau Brasil) (17°04'S, 39°31'W), 26 October 1969, Equipe Cepec-Ceplac (MNRJ 13101); *Goiás*: 1 ♀, Minaçú (Usina Hidrelétrica de Serra da Mesa) (14°02' S, 48°13'W), 9–20 December

1996, A. Franceschini (MCN 28002); *Espírito Santo*: 1 ♀, Vitória (Parque Moscoso) (20°19'S, 40°21'W), no date, no collector (MNRJ 3921); 1 ♂, Linhares (Reserva Biológica de Sooretama) (19°25'S, 40°04'W) no date, no collector (MNRJ 3922); *Rio de Janeiro*: 1 ♀, no date, no collector (MNRJ 1740); 2 ♀, Tanguá, Ipitangas (22°43'S, 42°43'W), 2 September 2001, E. Dubauskas (MNRJ 1737); *São Paulo*: 1 ♀, Amparo (22°41'S, 46°46'W), 1933, no collector (IBSP 398).

Diagnosis.—Males of *Macrinus pollexensis* resemble those of *M. succineus* by the presence of a retrolateral spiny field in the tegulum of the palp (Fig. 15). They are distinguished by the anterior bump in the curve of RTA (Figs. 14, 28, 29), by the narrow distal part of the tegulum (Fig. 29) and by the narrow serrated projection at the base of the embolus of the male palp (Fig. 18). Females are distinguished from the remaining *Macrinus* by the median septum of the epigynum, anteriorly truncated and longer than wide (Fig. 30) and by the narrower stalk of the spermathecae in the vulva (Fig. 31).

Description.—*Male* (NHMB 2262-a): prosoma orange, slightly darker at eye area; eye borders brown; clypeus brown; chelicerae orange; legs and pedipalps pale orange; sternum pale yellow with orange margins; labium orange, distally cream colored; endites pale yellow; opisthosoma pale yellow. Total length 13.3. Prosoma: 6.2 long, 6.0 wide. Eye diameters and interdistances: AME 0.44, ALE 0.34; PME 0.28, PLE, 0.3, AME–AME 0.2, AME–PLE 0.08, PME–PME 0.5, PME–PLE 0.4, AME–PME 0.36, ALE–PLE 0.24. Leg measurements: leg I: femur 10.6, patella 3.5, tibia 10.3, metatarsus 11.6, tarsus 3.2, total 39.2; leg II: femur 11.5, patella 3.6, tibia 11.3, metatarsus 12.0, tarsus 2.9, total 41.3; leg III: femur 9.4, patella 2.8, tibia 8.1, metatarsus 8.6, tarsus 2.3, total 31.2; leg IV: femur 10.4, patella 3.0, tibia 9.0, metatarsus 10.2, tarsus 2.4, total 35.0. Leg spination follows generic pattern, except femur IV: r0-1-1; tibia II: d0-0-1; tibia IV: d0-1-1. Palp: tegulum twisted with a retrolateral spiny field (Figs. 15, 29) and subrectangular serrated laminar projection at the base of the embolus (Fig. 18). Opisthosoma: 6.9 long, 4.5 wide.

Female (MNRJ 1739): coloration as in male. Total length 17.6. Prosoma: 8.1 long,

7.6 wide. Eye diameters and interdistances: AME 0.54, ALE 0.4, PME 0.4, PLE 0.32, AME–AME 0.36, AME–ALE 0.22, PME–PME 0.72, PME–PLE 0.65, AME–PLE 0.4, ALE–PLE 0.32. Leg measurements: leg I: femur 9.5, patella 4.0, tibia 8.4, metatarsus 8.8, tarsus 2.7, total 33.4; leg II: femur 10.0, patella 4.0, tibia 8.5, metatarsus 8.7, tarsus 2.5, total 33.7; leg III: femur 8.4, patella 3.3, tibia 6.5, metatarsus 6.2, tarsus 2.2, total 26.6; leg IV: femur 9.3, patella 3.2, tibia 6.8, metatarsus 7.4, tarsus 2.3, total 29.0. Leg spination follows generic pattern, except femora I–II: p1-1-0; femur IV: p0-1-0. Opisthosoma oval: 9.3 long, 6.5 wide. Epigynum: median septum anteriorly truncated, longer than wide (Fig. 30).

Variation.—Nine males: total length 10.1–13.9, prosoma length 4.9–6.5, femur I 9.0–10.8. Nine females: total length 13.9–22.3, prosoma 6.1–8.1, femur I 8.0–10.1.

Distribution.—Known from Northern and Eastern South America.

Macrinus jaegeri new species
Figs. 16, 33–38

Types.—BRAZIL: *Mato Grosso*: Male holotype from Usina Hidrelétrica de Guaporé, Vale São Domingos, Pontes e Lacerda (15°11'S, 59°22'W), October 1999, Equipe IBSP (IBSP 41494). Paratypes: BRAZIL: *Pará*: 1 female, collected with holotype (IBSP 41395); 1 ♂, Rio Tocantins, 2 km S. Jacundá (04°32'S, 49°28'W), 13 May 1984, W.L. Overall (MPEG 1011); 1 ♂, Estação Científica Ferreira Penna, Flona Caxiuanã, Melgaço (01°46'S, 50°43'W), 30 May–10 June 2002, M.C. Santos Costa (MPEG 490); *Mato Grosso*: 1 ♀, June 1971, J.H. Botelho (IBSP 2363); 1 ♂, Usina Hidrelétrica de Guaporé (15°11'S, 59°22'W), 23 May 2002, Operação Coatá (MCTP 13565); *Mato Grosso do Sul*: 1 ♀, Passo do Lontra, Corumbá (19°01'S, 57°38'W), July 1999, A.D. Brescovit (IBSP 23916).

Etymology.—The specific name honors Dr. Peter Jäger, for his contribution towards our understanding of sparassid systematics.

Diagnosis.—Males of *Macrinus jaegeri* are distinguished from those of the remaining *Macrinus* by the short, retrolateral projection on the tegulum of the male palp (Figs. 16, 34, 35). Females are distinguished by the median septum of the epigynum anteriorly truncated, as wide as long or slightly wider than long

(Fig. 36) and by the posteriorly widened spermathecal stalk (Fig. 31).

Description.—*Male (MPEG 1011)*: prosoma orange with median longitudinal brown stripe; chelicerae orange; legs and pedipalps orange; sternum pale orange with darker margins; labium dark orange, distally cream colored; endites pale orange, distally cream colored; opisthosoma pale yellow. Total length 15.9. Prosoma: 7.0 long, 6.4 wide. Eye diameters and interdistances: AME 0.48, ALE 0.4, PME 0.3, PLE 0.32, AME–AME 0.28, AME–ALE 0.12, PME–PME 0.3, PME–PLE 0.5, AME–PME 0.32, ALE–PLE 0.2. Leg measurements: leg I: femur 11.0, patella 3.8, tibia 11.0, metatarsus 12.8, tarsus 3.2, total 41.8; leg II: femur 11.8, patella 3.8, tibia 11.6, metatarsus 13.1, tarsus 3.2, total 43.5; leg III: femur 9.8, patella 3.3, tibia 8.7, metatarsus 9.0, tarsus 2.1, total 32.9; leg IV: femur 10.6, patella 3.1, tibia 9.2, metatarsus 11.0, tarsus 2.7, total 36.6. Leg spination follows generic pattern, except femora I–II: p1-1-0; femur IV p0-1-1. Opisthosoma oval: 8.6 long, 5.1 wide.

Female (IBSP 23916): coloration as in male. Total length 15.1. Prosoma: 6.6 long, 6.5 wide. Eye diameters and interdistances: AME 0.46, ALE 0.4, PME 0.26, PLE 0.34, AME–AME 0.32, AME–PLE 0.12, PME–PME 0.68, PME–PLE 0.54, AME–PME 0.4, ALE–PLE 0.34. Leg measurements: leg I: femur 8.7, patella 3.3, tibia 7.9, metatarsus 8.3, tarsus 2.4, total 30.6; leg II: femur 9.2, patella 3.6, tibia 8.0, metatarsus 8.5, tarsus 2.2, total 31.5; leg III: femur 7.5, patella 3.0, tibia 6.0, metatarsus 5.8, tarsus 1.6, total 23.9; leg IV: femur 8.0, patella 2.9, tibia 6.4, metatarsus 6.9, tarsus 1.9, total 26.1. Leg spination follows generic pattern. Opisthosoma oval: 8.2 long, 6.5 wide.

Variation.—Three males: total length 14.2–16.3; prosoma length 5.7–7.3; femur I 10.8–12.1. Three females: total length 14.3–15.1, prosoma length 6.6–8.8; femur I 8.6–11.6.

Distribution.—Known from central and northern Brazil.

ACKNOWLEDGMENTS

I wish to thank Antonio D. Brescovit, Adalberto J. Santos, and Peter Jäger for critical comments on this manuscript; Dr. Pedro Kyo-hara and Miss Simone Perche Toledo, from the Departamento de Microscopia Eletrônica

do Instituto de Física (LME-IF/USP), for making the scanning electron micrographs. This study was supported by the Ernst Mayr Grant, from the Museum of Comparative Zoology at Harvard University, the Theodore Roosevelt Memorial Fund and “Fundação de Amparo à Pesquisa de São Paulo” (Fapesp 99/05446-8; 02/11277-9). This paper is part of BIOTA-FAPESP – The biodiversity Virtual Institute (www.biotasp.org.br).

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Manuscript received 5 April 2006, revised 25 September 2006.

ARCTOSA STIGMOSA AND A. SUBAMYLACEA ARE TWO DIFFERENT SPECIES (ARANEAE, LYCOSIDAE)

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ABSTRACT. The Asian wolf spider *Arctosa subamylacea* (Bösenberg & Strand 1906), originally described from Japan, is currently treated as a junior synonym of the European *Arctosa stigmosa* (Thorell 1875). However, both species differ noticeably in genital and somatic morphology. Here, we remove *A. subamylacea* from its synonymy with *A. stigmosa* and redescribe both species from material recently collected in Asia and Europe. Both species differ in their habitat preferences, as *A. stigmosa* typically inhabits gravel and sandy habitats in alluvial river floodplains, whereas *A. subamylacea* lives in low vegetation near hills and in agricultural areas, sometimes near ponds and lakesides.

Keywords: Lycosinae, synonymy, morphological character, tegular apophysis

Wolf spiders (family Lycosidae Sundevall 1833) are distributed worldwide and represent a very diverse family of typically ground living spiders. Wolf spiders are easily recognized by their distinct eye arrangement, a notched trochanter and their mobile brood care (Dondale & Redner 1990), however the systematics and taxonomy of the group below the family level are still far from settled (Murphy et al. 2006). The genus *Arctosa* C.L. Koch 1848 represents a particularly puzzling systematic example. Recent molecular data could not confirm the traditional assumption that *Arctosa* is representative of the subfamily Lycosinae (e.g., Dondale 1986), and the genus may represent a new subfamily altogether (Murphy et al. 2006; see also Zehethofer & Sturmbauer 1998; Vink et al. 2002). The limitation of *Arctosa* itself has caused considerable controversy for quite some time (e.g., Braun 1963; Olinger et al. 2002) and, in particular, in relation

to Asian species, recent molecular data suggests that *Arctosa* does not represent a monophyletic taxon (Murphy et al. 2006; Park et al. 2007).

Arctosa subamylacea (Bösenberg & Strand 1906) was initially described from Japan and later regarded as a senior synonym of *Arctosa cervina* Schenkel 1936, originally described from China (Paik 1994). Earlier Zhang (1987) synonymized *A. cervina* with the European *A. stigmosa* (Thorell 1875) resulting in the current synonymy of *A. subamylacea* and *A. stigmosa* (Platnick 2007). However, the synonymy of both species has always been in dispute (Marusik et al. 2000; T. Kronestedt and H. Tanaka pers. comm.).

To elucidate the separate identities of *A. subamylacea* and *A. stigmosa* we examined representatives from across the known range of the taxa in Europe and Asia, including specimens from near the type localities of both species, i.e., Ukraine in the case of *A. stigmosa*, and Japan in the case of *A. subamylacea*. Despite close similarities the detailed comparison of somatic and genitalic

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characters revealed distinct and constant differences between specimens from Europe and Asia that warrant a refutation of Zhang's (1987) synonymy and a consideration of *A. stigmosa* and *A. subamylacea* as distinct species.

METHODS

We examined specimens collected in the countries from which both species were originally described, i.e., Ukraine (*A. stigmosa*) and Japan (*A. subamylacea*) and additional spiders from their putative ranges. Species descriptions are based on specimens preserved and examined in 75% alcohol under an Olympus SZH10 stereomicroscope. For scanning electron microscope photography with a Leo 1420VP scanning electron microscope (Carl Zeiss, Oberhofen/Germany), a dissected right pedipalp of *A. subamylacea* (lodged at NIAST) was fixed with Karnovsky's fixative and osmic acid, and sputter coated with gold. Morphological nomenclature follows Framenau & Yoo (2006). All measurements are in millimeters (mm) and are based on adult spiders.

Abbreviations.—Measurements (in mm): total length (TL), carapace length (CL) and width (CW), abdomen length (AL) and width (AW). Eyes: anterior row of eyes (AER), anterior median (AME), anterior lateral (ALE), posterior row of eyes (PER), posterior median (PME), posterior lateral (PLE). QPE = quadrangle of posterior eyes. Collections: ASJ = Arachnological Society of Japan, Otemon Gakuin University, Osaka, Japan; IKAS = Institute of the Korean Arachnological Society, Namyangju-si, Korea; NIAST = National Institute of Agricultural and Technology, RDA, Suwon-si, Korea; SMF = Senckenberg Museum, Frankfurt, Germany; SMNH = Swedish Museum of Natural History, Stockholm, Sweden; WAM = Western Australian Museum, Perth, Australia; ZMB = Museum für Naturkunde, Zentralinstitut der Humboldt-Universität, Berlin, Germany; ZMH = Zoologisches Institut und Zoologisches Museum, Universität Hamburg, Germany.

TAXONOMY

Lycosidae Sundevall 1833

Arctosa C.L. Koch 1847

Type species.—*Aranea cinerea* Fabricius 1777, by subsequent designation of Simon (1937).

Diagnosis (after Dondale & Redner 1983 and Paik 1994).—Medium to large spiders (5–16 mm). Carapace broad, rather low, and approximately even in height between median furrow and posterior eye row; coloration grayish-brown to black or mottled with gray or brown without properly defined longitudinal light bands. Chelicerae with two or three promarginal teeth and three retromarginal teeth. Abdomen usually pale and mottled, similar in color to carapace. Tegular apophysis of male pedipalp prominent, sclerotized, elongate, grooved or excavated on distal surface. Terminal apophysis conspicuous, in two parts or in one part, sometimes in different degrees of sclerotization. Embolus straight or curved. Epigynum of female usually with conspicuous atrium divided by median septum, no anterior hoods.

Arctosa stigmosa (Thorell 1875)

Figs. 1–5, 11, 12

Trochosa stigmosa Thorell 1875a:107–108; Thorell 1875b:175–176; Chyzer & Kulczyński 1891:74, pl. 3, fig. 13.

Lycosa stigmosa (Thorell): Simon 1876:280.

Lycosa vigilans L. Koch 1881:69–71, fig. 13 (synonymy established in Dahl 1908).

Arctosa stigmosa (Thorell): Dahl 1908:308, 321, fig. 38; Lugetti & Tongiorgi 1966:139–141, fig. II (1–4); Fuhn & Niculescu-Burlacu 1971:187–189, figs. 92a–e; Miller 1971:165, pl. 25, fig. 29, pl. 36, fig. 2; Loksa 1972:55, fig. 49C–D; Heimer & Nentwig 1991:320, fig. 855; Aakra 2000:157, figs. 3A–B, 4.

Arctosa turbida Rosca 1935: 252–254, figs. 11–12 (synonymy established in Fuhn & Niculescu-Burlacu 1971).

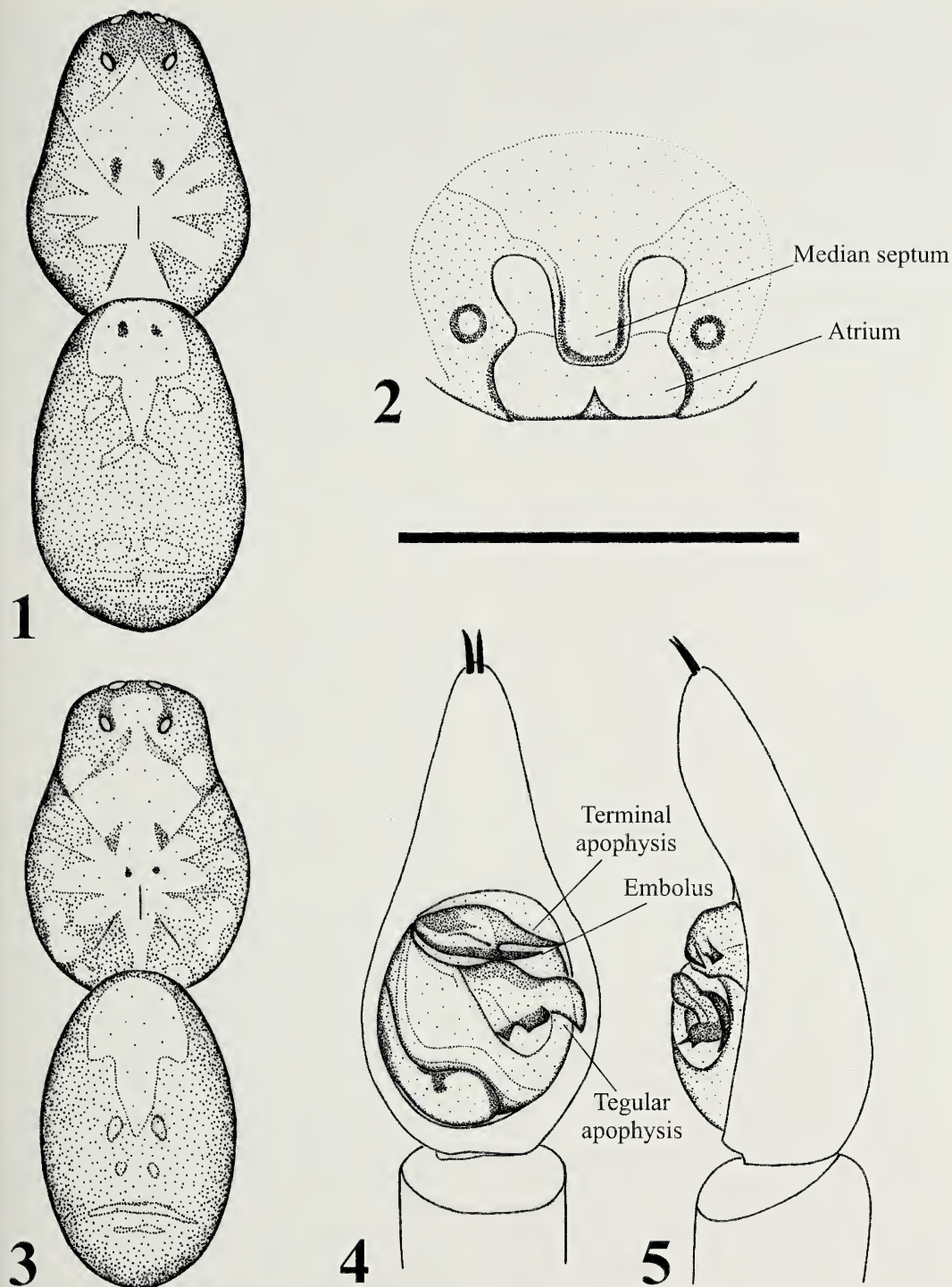
Lycosa turbida (Rosca): Roewer 1955:270.

Cynosa stigmosa (Thorell): Roewer 1955:239.

Type specimens.—*Trochosa stigmosa*: holotype female, UKRAINE: *Dnipropetrovsk Oblast*: Dnipropetrovsk (ca. 48°28'N 35°00'E), Al. v. Nordmann (Thorell 1875a) [depository unknown. The specimen is not present in SMNH or Zoological Museum of the University, Helsinki where Thorell's (1875a) types are expected to be housed, T. Kronstedt pers. comm.].

Lycosa vigilans: holotype female, GERMANY: *Saxonia*: near Niesky (ca. 51°17'N 14°49'E) [depository unknown; seen by Dahl 1908; not in ZMB (Moritz 1992) or ZMH (Rack 1961)].

Arctosa turbida: unknown number of syn-type males and females, ROMANIA: *Sereth*:



Figures 1–5.—*Arctosa stigmosa* (Thorell), male and female from Norway (SMNH): 1. Female, dorsal view; 2. Epigynum, ventral view; 3. Male, dorsal view; 4. Male, left pedipalp, ventral view; 5. Left pedipalp, retrolateral view. Scale bar: 3.87 mm (Fig. 1); 0.25 mm (Fig. 2); 4.08 mm (Fig. 3); 0.72 mm (Figs. 4, 5).

Horaitz, Bălcauți (47°54'N 26°05'E), Calafindești (47°51'N 26°07'E) (Rosca 1935) (depository unknown; the study was carried out at the Zoological Institute of the University of Chernivtsi, Ukraine).

Material examined.—NORWAY: *Sør-Trøndelag*: 1 ♂, 1 ♀, Melhus, Gauldal (63°16'N, 10°16'E), 5 April 1994, K. Aakra (SMNH). GERMANY: *Bavaria*: 1 ♀, 1 juvenile, Isar River near Vorderriß (river-km 241) (47°34'N, 11°25'E), 16 August 1994, R. Manderbach (WAM T56418); 1 ♀, same locality, 15 June 1995, R. Manderbach (WAM T56419); 1 ♂, same locality, 26 August 1994, R. Manderbach (WAM T56420); 1 ♂, same locality, 15 June 1995, R. Manderbach (WAM T56421); 1 ♂, Isar River near Vorderriß (river-km 242) (47°34'N, 11°26'E), 2 September 1994, VWF (WAM T56422); 1 ♂, same locality, 20 May 1994, VWF (WAM T56423); 1 ♂, same locality, 13 June 1994, VWF (WAM T56424); 1 ♂, 1 juvenile same locality, 17 June 1994, VWF (WAM T56425); 1 ♂, Isar River near Schroefeln (47°33'N, 11°23'E), 1 August 1994, R. Manderbach (WAM T56426); 1 ♂, same locality, 31 August 1994, R. Manderbach (WAM T56427); 1 ♀, same locality 1 August 1994, R. Manderbach (WAM T56428); 1 ♂, same locality, 3 August 1994, R. Manderbach (WAM T56429); 1 ♂, 1 juvenile, same locality, 8 September 1994, R. Manderbach (WAM T56430). UKRAINE: *Lvivska Oblast*: 1 ♂, Dnister River, SE Sambir (49°28'N, 23°03'E), 21 September 1995, S. Niemeyer (WAM T66627); 1 ♂, same locality, 12 September 1995, S. Niemeyer (WAM T66628); 1 ♀, same locality, 5 August 1995, S. Niemeyer (WAM T62737); 1 ♂, same locality, 1 September 1995, S. Niemeyer (WAM T66629); 1 ♀, same locality, 4 August 1995, S. Niemeyer (WAM T66625).

Diagnosis.—Tegular apophysis of male pedipalp with one distinctly larger protrusion at retrolateral base and a few reduced protrusions on prolateral lobe (Figs. 11, 12). Median septum of epigynum straight, without round or hollow parts (Fig. 2). Maple-leaf-shaped median pattern on the carapace (Figs. 1, 3).

Description.—*Male (based on specimen from Gauldal, Norway)*: Carapace dark brown, covered with slanted white setae; dark, radial pattern indistinct; median light band maple-leaf-shaped occupying over one half of carapace width and extending from behind

PLE to the end of dark median groove (Fig. 3); light spots present near lateral margins but almost fused to light median band. AER nearly straight in frontal view and slightly shorter than PMR; AME larger than ALE. QPE wider than long (ratio 100:148). Clypeus height similar to the diameter of AME. Chelicerae dark brown. Endites basally brown, apical part off-white with pale edge. Labium dark brown, re-bordered whitish. Sternum dark brown with lighter edge, sparse black, erect setae that are denser at margins. Legs light brown, with dark brown annulations except tarsi I–IV; coxae light brown dorsally and yellowish-brown ventrally. Leg formula 4123. Spination of leg I: femur: 3 dorsal (apical spine small), 1 apicoprolateral; tibia: 2 prolateral (sometimes 1 apicoprolateral), 2 ventral pairs; metatarsus: 1 prolateral, 2 ventral pairs and 3 apicoventral. Abdomen dorsally gray; yellow-brown lanceolate cardiac mark with irregular markings (Fig. 3); venter yellowish-brown without pattern. Spinnerets yellowish-brown. Pedipalp with two macrosetae at cymbium tip; terminal apophysis and embolus exposed ventrally; tegular apophysis prominent, sclerotized, transversely elongated and curved basally (Figs. 4, 5).

Female (based on specimen from Gauldal, Norway): Somatic characters and coloration similar to those of male (Fig. 1). Epigynum: median septum quadrangular, lateral edges almost parallel to each other; lateral edges of atrium depressed at the center (Fig. 2).

Measurements: male (female) (both based on specimens from SMNH): TL 6.56 (6.21), CL 3.42 (2.85), CW 2.49 (2.14). Eyes: AME 0.12 (0.11), ALE 0.09 (0.10), PME 0.25 (0.22), PLE 0.22 (0.17). Row of eyes: AE 0.62 (0.57), PME 0.67 (0.60), PLE 0.88 (0.84). Sternum (length/width) 1.27/1.48 (1.36/1.20). Labium (length/width) 0.43/0.40 (0.36/0.45). AL 3.42 (3.14), AW 2.35 (2.07). Pedipalp: Length of segments (femur + patella/tibia + tarsus = total length): 1.19 + 0.95 + 0.90 = 3.04 (1.19 + 1.09 + 0.76 = 3.04). Legs: Lengths of segments (femur + patella/tibia + metatarsus + tarsus = total length): I 2.28 + 2.85 + 1.90 + 1.19 = 8.22, II 2.18 + 2.47 + 1.71 + 1.04 = 7.40, III 1.99 + 2.04 + 1.66 + 1.04 = 6.73, IV 2.76 + 2.90 + 2.52 + 1.28 = 9.46 (I 1.85 + 2.23 + 1.42 + 0.95 = 6.45, II 1.66 + 2.09 + 1.38 + 0.95 = 6.08, III 1.71

+ 1.90 + 1.42 + 0.90 = 5.93, IV 2.38 + 2.76 + 2.28 + 1.19 = 8.61).

Distribution.—Central Europe (including Bulgaria, France, Germany, Norway, Romania, Switzerland, Ukraine) (Fuhn & Niculescu-Burlacu 1971; Heimer & Nentwig 1991; Aakra & Hauge 2000).

Habitat preferences.—Most common in gravel and sandy habitats in alluvial river floodplains (Framenau et al. 1996; Aakra 2000; Aakra & Hauge 2000); also reported from sandy, dry grasslands (Rosca 1935). Adults in March to July and October (Heimer & Nentwig 1991).

Arctosa subamylacea
(Bösenberg & Strand 1906)
Figs. 6–10, 13–17

Tarentula subamylacea Bösenberg & Strand 1906: 322, pl. 13, fig. 318.

Lycosa subamylacea (Bösenberg & Strand): Saito, 1959:55, figs. 36 a–b.

Arctosa cervina Schenkel 1936:191–194, fig. 63; Song 1982:75, figs. 1–2; Hu & Wu 1989:197, fig. 164.1–6; Chen & Zhang 1991:219, fig. 226.1–4; Zhao 1993:63, fig. 24a–c; Eskov & Marusik 1995:77, fig. 57; Marusik et al. 2000:80 (synonymy established in Paik 1994).

Avicosa cervina (Schenkel): Roewer 1955:234.

Hoggicosa subamylacea (Schenkel): Roewer 1955: 247.

Arctosa subamylacea (Bösenberg & Strand): Yaginuma 1960:85, fig. 76.6; Chikuni 1989:111, fig. 9; Tanaka 1991:308–311, figs. 29–32; Paik 1994: 41–44, figs. 9–19.

Arctosa kobayashii Yaginuma 1960: app. 6, plate 40, fig. 225, fig. 76.7; Yaginuma 1971:85, fig. 76.7 (synonymy established in Yaginuma 1986).

Arctosa stigmata (Thorell): Zhang 1987:145–147, figs. 121.1–4; Song et al. 1999:319–320, figs. 190D, R; Namkung 2002:316, figs. 20.10a–b; Kim & Cho 2002:205, figs. 433–438 (not *A. stigmata* sensu Thorell 1875a)

Type specimens.—*Tarentula subamylacea*: holotype female, JAPAN: *Saga Prefecture*: (ca. 33°14'N, 130°17'E): 1882, Dönitz (SMF 2198).

Arctosa cervina: holotype female, PEOPLES REPUBLIC OF CHINA: *South Kansu* (=Jansu): Tan-chang (ca. 36°05'N, 103°68'E), 28 September 1930, D. Hummel (SMNH).

Arctosa kobayashii: holotype female, JAPAN: *Tokushima Prefecture*: Tokushima-shi, Shikoku (34°03'N, 134°33'E), paddy field, 17 May 1957, Kobayashi (ASJ).

Material examined.—KOREA: *Kyonggi-*

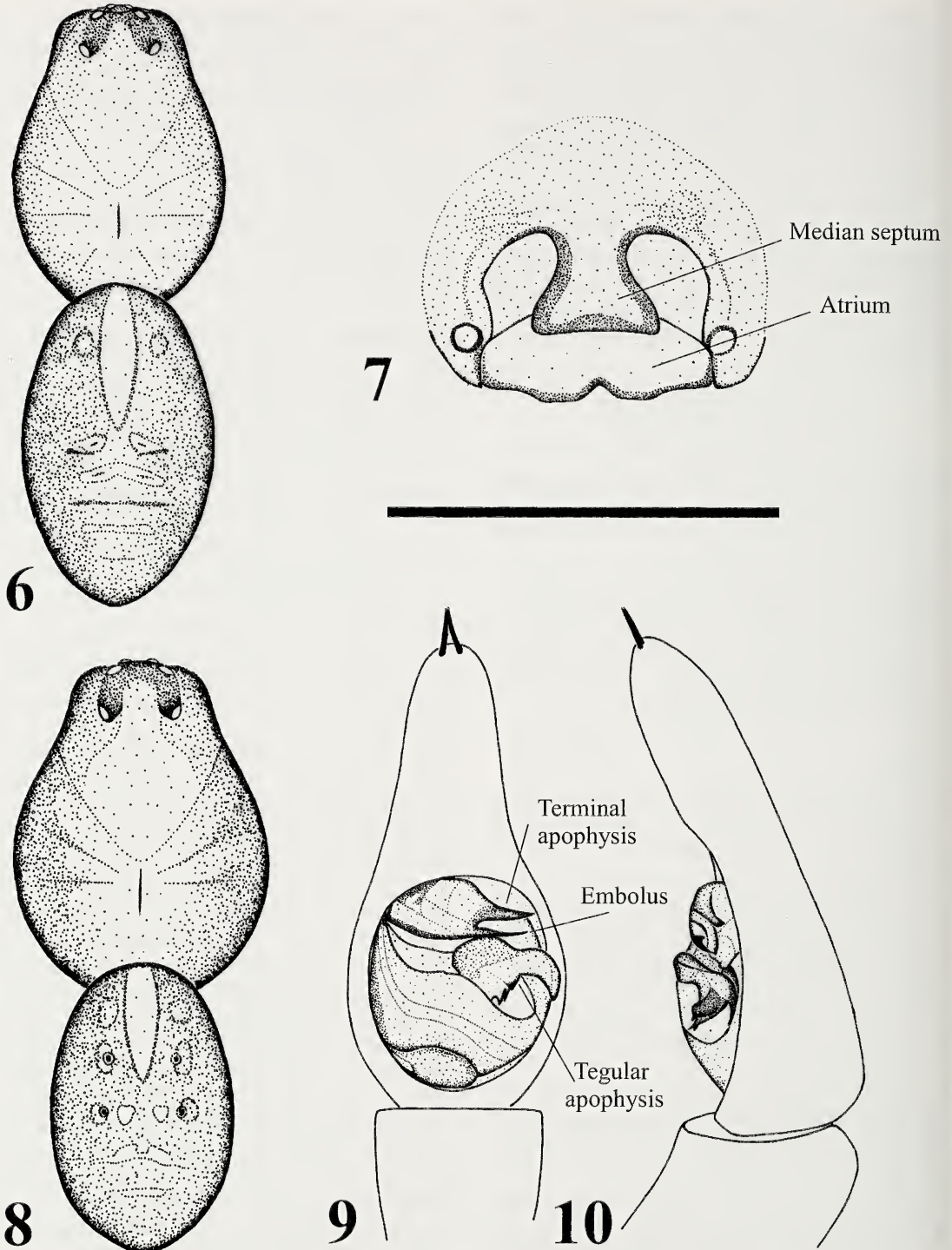
do: 1 ♀, Suwon-city (33°42'N, 126°26'E), 25 July 2003, JSY (WAM T62745); 1 ♀, same locality, 6 August 1999, JSY (WAM T62751); 1 ♂, Yeosu-gun, Ulkeuk-ri (37°25'N, 127°61'E), 25 November 1998, JSY (WAM T62754); 1 ♂, Yeoncheon-gun, Chungok-eup, Yeonderi (38°13'N, 126°91'E), 15 June 1999, JSY (WAM T62755); 2 ♀, same locality, 15 June 1999, JSY (WAM T62756). JAPAN: *Shiga-ken* (*Honshu*): 2 ♂, 1 ♀, Otsu-city (35°00'N, 135°52'E), 9 June 1997, H. Tanaka (WAM T66632–4).

Diagnosis.—Tegular apophysis of male pedipalp with several small protrusions at the base, of which the middle one is generally the largest (Fig. 13, 14). Median septum of epigynum comparatively wider than that of *A. stigmata* and widest posteriorly (Fig. 7).

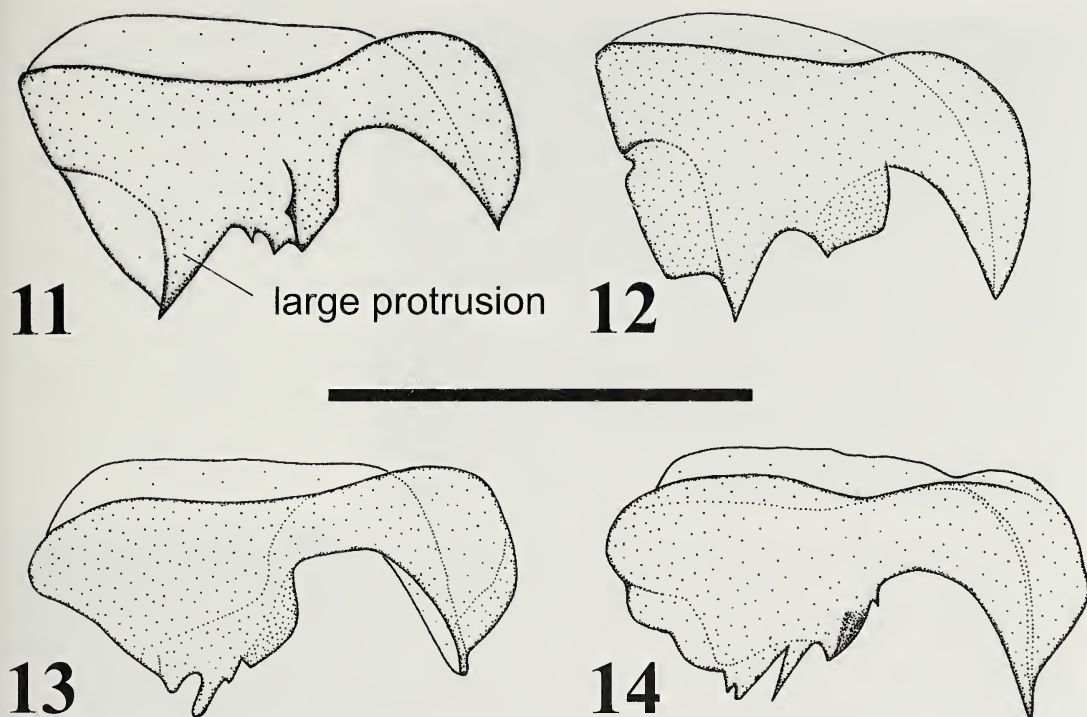
Description.—*Male* (from Otsu-city, Japan, WAM T66634): Carapace dark brown (Fig. 8), laterally covered with slanted short white setae; radial pattern indistinct gray; center of carapace lighter; submarginal bands dissolved into mottled vestiges, which almost fuse to the lighter median part. PME on a black, inverted U-shaped pattern. AER nearly straight in frontal view and slightly shorter than PMR; AME larger than ALE. QPE wider than long (ratio 100:148). Clypeus height equal to the diameter of AME. Chelicerae dark brown. Basal half of endites dark brown, apical half brown. Labium dark brown and palely rebordered. Sternum brown, sparsely covered with dark, erected and long setae that are denser near the margins. Legs dark brown, femora lighter, coxae brown; light annulations on femora, tibiae and metatarsi. Leg formula, 4123. Spination of leg I: femur: 3 dorsal (apical one small), 1 apicoprolateral; tibia: 2 dorsal, 2 ventral pairs; metatarsus: 2 ventral pairs and 3 apicoventral. Abdomen dark gray with a pale brown lanceolate cardiac mark which is surrounded by pale brown tiny spots; venter uniformly yellow. Spinnerets yellowish. Pedipalp with two macrosetae at cymbium tip; terminal apophysis and embolus sickle shape; tegular apophysis with one lobe with a few small protrusions.

Female (from Otsu-city, Japan, WAM T66632): Somatic characters and coloration are similar to those of male (Fig. 6). Epigynum: median septum widest at posterior end.

Measurements: male, WAM T66634 (female, WAM T66632): TL 6.92 (9.11), CL



Figures 6–10.—*Arctosa subamylacea*: (Bösenberg & Strand), males and females from Japan and Korea: 6. Female, dorsal view (WAM T66632); 7. Epigynum, ventral view (T62756); 8. Male, dorsal view (T66634); 9. Male, left pedipalp, ventral view (T62755); 10. Left pedipalp, retrolateral view (T62755). Scale bar: 5.52 mm (Fig. 6); 0.68 mm (Fig. 7); 4.57 mm (Fig. 8); 0.80 mm (Figs. 9, 10).



Figures 11–14.—Tegular apophyses of left male pedipalp in ventral view: 11, 12. *A. stigma* from 11. Ukraine (WAM T66628), 12. Norway (SMHN); 13, 14. *A. subamylacea* from 13. Korea (WAM T62754) and 14. Japan (WAM T66634). Scale bar: 6.82 mm.

3.99 (4.42), CW 3.07 (3.14). Eyes: AME 0.15 (0.16), ALE 0.11 (0.11), PME 0.27 (0.31), PLE 0.25 (0.28). Row of eyes: AE 0.62 (0.84), PME 0.64 (0.86), PLE 0.88 (1.17). Sternum (length/width) 1.46/1.77 (1.58/1.92). Labium (length/width) 0.57/0.52 (0.60/0.55). AL 3.42 (4.64), AW 2.57 (3.14). Pedipalp: Length of segments (femur + patella/tibia + tarsus = total length): 1.38 + 1.19 + 1.09 = 3.66 (1.61 + 1.60 + 1.14 = 4.35). Legs: Length of segments (femur + patella/tibia + metatarsus + tarsus = total length): I 2.61 + 3.04 + 2.09 + 1.19 = 8.93, II 2.38 + 2.85 + 1.95 + 1.09 = 8.27, III 2.28 + 2.42 + 1.90 + 1.14 = 7.74, IV 2.95 + 3.52 + 3.18 + 1.57 = 11.22 (I 2.76 + 3.33 + 1.99 + 1.33 = 9.41, II 2.47 + 3.04 + 1.90 + 1.33 = 8.74, III 2.42 + 2.71 + 2.33 + 1.19 = 8.70, IV 3.47 + 4.18 + 3.71 + 1.61 = 12.97).

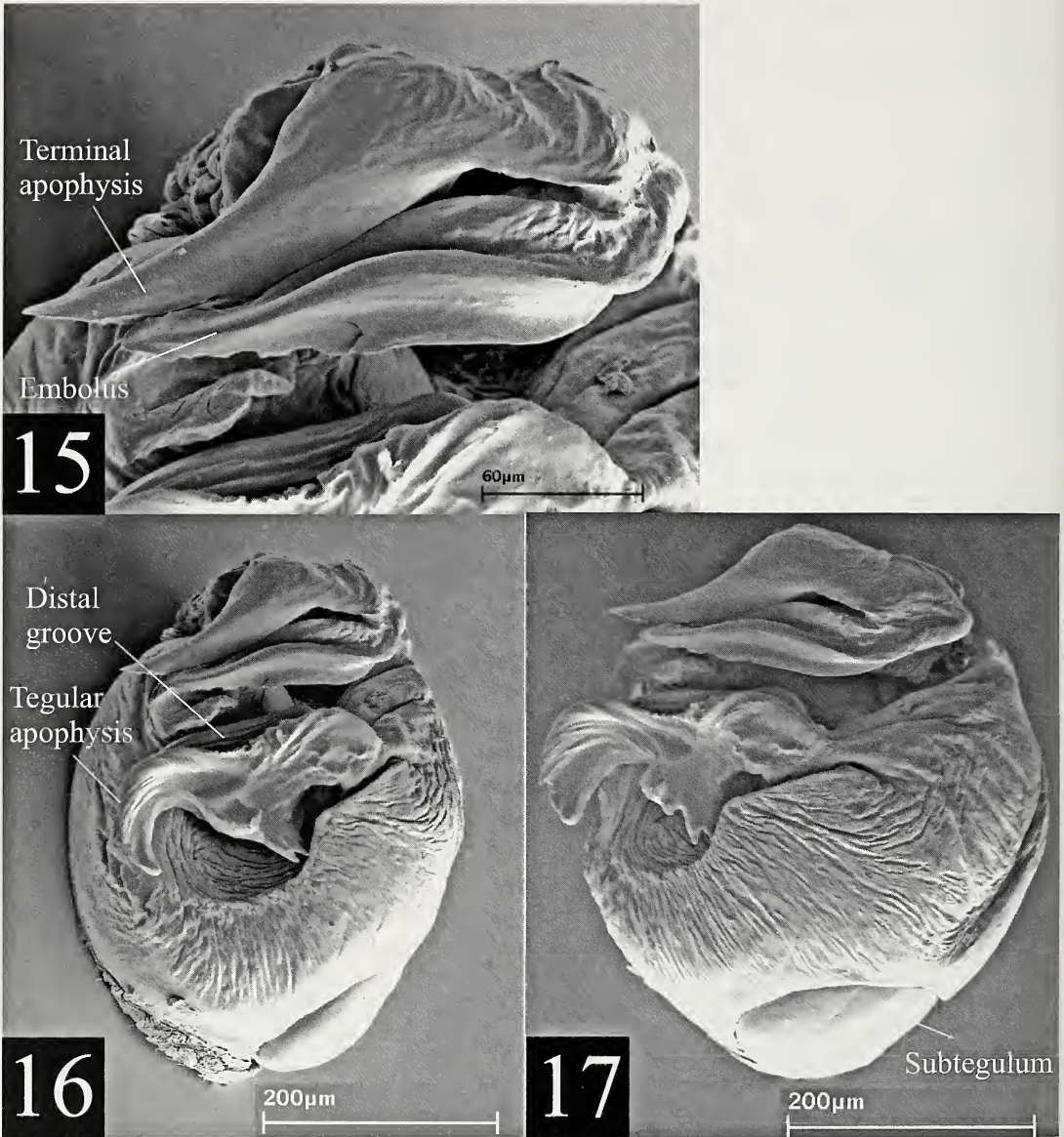
Distribution.—China, Japan, Kazakhstan, Korea (Paik 1994; Marusik et al. 2000)

Habitat preferences.—Common in habitats with low vegetation, such as meadows and grasslands. It is particularly common in agricultural areas such as near rice fields.

DISCUSSION

Arctosa stigma and *A. subamylacea* are very similar species and differences in the genitalia are very subtle. Similar to wolf spiders within the subfamily Lycosinae, males of both species have prominent and transverse tegular apophyses with a groove on the distal surface. The tip of the tegular apophysis is directed basally. The terminal apophysis is well developed and sickle-shaped (Figs. 4, 9). The embolus is transverse and not covered by the tegular apophysis in ventral view (Figs. 15–17). The epigynum has a conspicuous atrium divided by a median septum, but no distinct anterior hoods (Figs. 2, 7).

However, *A. stigma* and *A. subamylacea* are separated as distinct species by the following characters: (a) the basal edge of the tegular apophysis of the male pedipalp has one large, shark-tooth like protrusion at the base of the apophysis and a smaller lobe with small teeth retrolaterally from it in *A. stigma* (Figs. 11, 12), while in *A. subamylacea* the base appears as one lobe with a few small



Figures 15–17.—*Arctosa subamylacea* (Bösenberg & Strand) from Korea (NIAST): 15. Embolic division, ventral view; 16. Bulb of pedipalp, retrolateral view; 17. Bulb of pedipalp, ventral view.

separate protrusions (Figs. 13, 14); (b) the configuration of the median septum in female epigyna differs in the two species, although the variations may overlap. Overall, the posterior edge of median septum in all examined *A. subamylacea* is relatively wider than that of *A. stigmosa*; (c) the presence of maple-leaf-shaped median pattern on carapace in *A. stigmosa* (Figs. 1, 3), and (d) the lanceolate cardiac mark of *A. subamylacea* (Figs. 6, 8).

The habitat preferences of *A. stigmosa* and

A. subamylacea differ considerably although little is known of the ecology of these two species. *Arctosa stigmosa* is a riparian spider and appears to be confined to sand and gravelly riverbanks and is therefore closely associated with alluvial floodplains. It probably spends the day in litter close to the river banks (Dahl 1908; Framenau et al. 1996; Aakra 2000; Aakra & Hauge 2000). In contrast, *A. subamylacea* may be seen near ponds or lake-shores (Marusik et al. 2000), but it is com-

monly collected in agroecosystems and hilly environments in grassy vegetation (Paik 1994; JSY and KJP pers. obs.).

ACKNOWLEDGMENTS

We are grateful to Torbjörn Kronestedt (SMNH) and Hozumi Tanaka (Sonoda Women's College) for the loan or donation of specimens and useful discussions in relation to this study. Young-Bo Lee and An-Ja Ko (National Institute of Agricultural Science and Technology, Suwon, Korea) took the SEM photographs. Bill Humphreys (WAM) kindly permitted the use of his stereomicroscope. We are particularly grateful to Torbjörn Kronestedt and Mark Harvey for comments on earlier drafts of this manuscript. This work was supported by the Korean Research Foundation Grant funded by the Korean Government (MOEHRD) (KRF-2005-214-C00226) (to Jung-Sun Yoo). Volker W. Framenau received financial support through the Australian Biological Resources Study (ABRS).

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Manuscript received 11 May 2006, revised 22 August 2006.

ASSOCIATION OF TWO NEW *CORYPHASIA* SPECIES (ARANEAE, SALTICIDAE) WITH TANK-BROMELIADS IN SOUTHEASTERN BRAZIL: HABITATS AND PATTERNS OF HOST PLANT USE

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ABSTRACT. Two allopatric species of *Coryphasia* (Araneae: Salticidae), both described for the first time in this study, have been found associated with Bromeliaceae in distinct phytophysiognomies (e.g., inselbergs, highland forests and restingas) from southeastern Brazil. In this study, we investigated whether these salticids were associated specifically with bromeliads, and whether they used bromeliads of different species and sizes in distinct geographic regions. The *Coryphasia* species were rarely found outside bromeliads, occupied larger bromeliad species among those available, and were generally more frequent on bromeliads in open areas, such as inselbergs on mountain tops. The two *Coryphasia* species were observed submerging in phytotelmata, possibly as an anti-predatory behavior. The patterns of spatial and microspatial distribution and the submergence behavior of these species were similar to those of other bromeliad-dwelling salticids, which suggests a convergence among spiders that live on bromeliads.

Keywords: Animal-plant interactions, Bromeliaceae, spider, specific association, submergence behavior, phytotelmata

Plants of the family Bromeliaceae are almost exclusively neotropical and are frequently inhabited by a large variety of aquatic and terrestrial arthropods (Benzing 2000). Some spiders are specifically associated with bromeliads in South and Central America, and use these plants as foraging and mating sites, nurseries, and shelter against predation and climatic extremities (Barth et al. 1988a,b; Baurecht & Barth 1992; Dias et al. 2000; Rossa-Feres et al. 2000; Santos et al. 2002; Dias & Brescovit 2003, 2004; Romero & Vasconcellos-Neto 2004, 2005a,b,c; Romero 2006). All known species of neotropical wandering spiders of the genus *Cupiennius* (Ctenidae), for example, are closely associated with par-

ticular plants, especially the Bromeliaceae and Musaceae, on which they hide during the day and prey, mate, and molt during the night (Barth et al. 1988b). *Cupiennius salei* (Keyserling 1877) lives in close association with some bromeliad species (Barth & Seyfarth 1979; Barth et al. 1988b), and uses vibratory signals to communicate during courtship on the host plant (Barth et al. 1988a; Baurecht & Barth 1992). *Pachistopelma rufonigrum* Pocock 1901 (Theraphosidae) is also strictly associated with the tank-bromeliad *Hohenbergia ramageana* Mez. in northeastern Brazil, and probably uses these plants as a shelter against the high temperatures of the sandy soil and as nurseries (Dias et al. 2000; Santos et al. 2002; Dias & Brescovit 2003, 2004).

Recent studies have reported strict associations between jumping spiders and bromeliads (Rossa-Feres et al. 2000; Romero & Vasconcellos-Neto 2004, 2005a,b,c; Romero 2006). For instance, *Psecas chapoda* (Peck-

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ham & Peckham 1894) inhabits exclusively *Bromelia balansae* Mez., a terrestrial bromeliad that does not accumulate rain water, in several regions of Brazil, Paraguay and Bolivia (Rossa-Feres et al. 2000; Romero & Vasconcellos-Neto 2005a,b,c; Romero 2006). The entire life cycle of this species, including courtship behavior, mating, oviposition, and the population recruitment of immatures, occurs on this plant (Rossa-Feres et al. 2000; Romero & Vasconcellos-Neto 2005b). Whereas the leaves are used as foraging and mating sites, the base of the rosettes serves as a shelter and resting site, and the center of the bromeliads is used as a nursery (Romero & Vasconcellos-Neto 2005a,c). *Eustiromastix nativo* Santos & Romero 2004, and undescribed species of *Psecas* and *Uspachus* are also strictly associated with tank-bromeliads in southeastern and northeastern Brazil (Romero 2006), and probably use bromeliads as shelters against predators and high temperatures, as well as foraging and egg laying sites (Romero & Vasconcellos-Neto 2004). *Eustiromastix nativo* inhabits the larger bromeliads among those available, which suggests that this species may assess the physical state of its microhabitats (Romero & Vasconcellos-Neto 2004).

Two undescribed *Coryphasia* species have been found inhabiting some bromeliad species on mountain tops (inselbergs) and in highland forests and restingas (a sandy soil forest, common at the Brazilian coast) in distinct geographic regions of southeastern Brazil. These species are described and illustrated here for the first time, along with several details of their natural history. To understand the spider-plant relationships of these species, we addressed the following questions: 1) Are these *Coryphasia* species strictly associated with bromeliads? 2) Do these spiders occur more on bromeliads of larger size? and 3) Do these spiders inhabit all of the available bromeliad species with the same frequency? Additionally, anti-predatory behavior of these salticids are described.

METHODS

This study was done at four localities in southeastern Brazil: at a rocky, open site (inselberg) on a mountain top (elevation ~1900 m) and in an adjacent Atlantic rain forest near the town of Monte Verde (22°51'S, 46°20'W),

in Minas Gerais state, from August to October 2003, and in December 2004 and April 2005; on an inselberg of Sugar Loaf mountain (Pão de Açúcar, 22°57'S, 43°09'W), in Rio de Janeiro city, Rio de Janeiro state, from April to May 2004, and in a restinga (i.e., plant communities on sandy soil close to the shore, Lacerda et al. 1984) in the Ilha do Cardoso State Park (Parque Estadual da Ilha do Cardoso, 25°03'S, 47°53'W), an island located on the coast of São Paulo state, in April 2005. Additional observations were done in a tropical, semideciduous forest (elevation ~1000 m) in the Ecological Reserve of the Serra do Japi (23°11'S, 46°52'W), Jundiaí city, São Paulo state.

In Monte Verde, the bromeliads *Aechmea distichantha* Lem., *Nidularium innocentii* Lem. and *Vriesea bituminosa* Wawra were very common in the forest understory and were similar in leaf length and number of leaves (Table 1), although the first of these has a uniquely lithophytic habit, inhabits open areas of granitic rock in inselbergs, and has conspicuous spines along the leaf edges. In Rio de Janeiro, the bromeliad species found were *Alcantarea glaziouana* (Lemaire) Leme and *Neoregelia cruenta* (R.Graham) L.B.Smith, both of which inhabited only open areas of the granitic rocks on the inselberg (absent in forest), although only the latter had spines at their leaf edges. At Ilha do Cardoso, the bromeliad species found were *Quesnelia arvensis* (Vell.) Mez, *Aechmea nudicaulis* (L.) Griseb. and *Vriesea carinata* Wawra, and all occurred in shady environments (restinga understory); the first two species bore small spines and the latter had no spines along the leaf margins. In the Serra do Japi, the only terrestrial bromeliad encountered was *Bromelia antiacantha*; this species was the only one of all the bromeliads that did not form phytotelmata (i.e., tank that hold rain water).

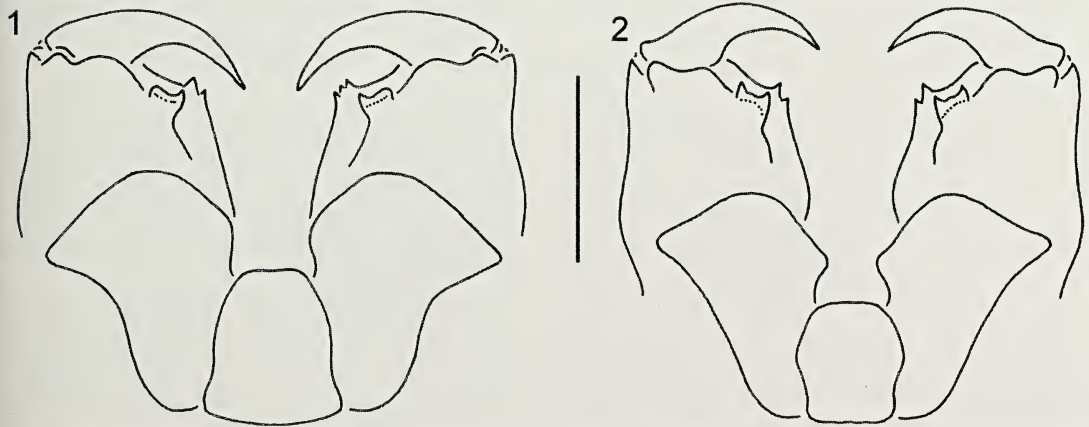
Two salticid species were collected on these bromeliad species, *Coryphasia monteverde*, a new species from Monte Verde and Serra do Japi, and *Coryphasia cardoso*, new species from Rio de Janeiro and Ilha do Cardoso. Both species are certainly members of the genus *Coryphasia*, which can be distinguished from other members of the subfamily Euphryinae by the presence of a bifid tooth on the posterior margin of the chelicerae, a lateral process on the endites (Figs. 1, 2), and the

Table 1.—Mean (± 1 SE in cm) of leaf length (LL), leaf base breadth (LB) and number of leaves (NL) for each bromeliad species at Monte Verde, Rio de Janeiro and Ilha do Cardoso. N = number of plants measured. Different letters indicate significant differences ($P < 0.05$, ANOVA/Tukey post hoc test for data from Monte Verde and Ilha do Cardoso, and Student t -test for data from Rio de Janeiro).

Bromeliad species	LL	LB	NL	N
Monte Verde				
<i>Aechmea distichantha</i>	29.76 \pm 2.06 a	3.95 \pm 0.23 a	23.35 \pm 1.31 a	18
<i>Nidularium innocentii</i>	36.03 \pm 1.54 a	3.62 \pm 0.18 a	21.33 \pm 1.16 a	16
<i>Vriesea bituminosa</i>	36.53 \pm 3.55 a	7.47 \pm 0.33 b	19.12 \pm 1.33 a	17
Rio de Janeiro				
<i>Alcantarea glaziouana</i>	33.89 \pm 0.90 a	10.0 \pm 0.18 a	25.07 \pm 1.12 a	81
<i>Neoregelia cruenta espinhos</i>	20.12 \pm 1.01 b	7.04 \pm 0.24 b	16.64 \pm 0.93 b	25
Ilha do Cardoso				
<i>Vriesea carinata</i>	65.00 \pm 4.86 a	6.80 \pm 0.22 a	24.70 \pm 1.53 a	10
<i>Quesnelia arvensis</i>	40.60 \pm 2.00 b	6.02 \pm 0.20 b	26.30 \pm 2.22 a	10
<i>Aechmea nudicaulis</i>	44.40 \pm 2.70 b	5.27 \pm 0.18 c	6.80 \pm 0.25 b	10

male palpus without apical sculpturing on the embolus (Edwards et al. 2005). So far this genus contains eight species, all described from Brazil (Platnick 2006). After comparing the material collected in this study with recent illustrations of all species of the genus (Galiano 1963; Bauab Vianna 1986; Rinaldi & Avelino 2000; Edwards et al. 2005), we concluded that both species were unknown to science, and have therefore described them here. The description format follows that of Santos & Romero (2004), with all of the measurements in mm. The material examined was deposited in the spider collection of the Instituto Butantan, São Paulo, Brazil (IBSP, curator A.D. Brescovit).

We investigated whether the *Coryphasia* spp. were strictly associated with bromeliads or whether they also occurred on other plants. For this, we inspected the leaves (underside and upper side) and stems of herbaceous plants and shrubs (non-bromeliads) with a total height of up to 1.7 m; the branches and trunks of taller plants were inspected at a height of up to 1.7 m. The inspections were done between 9:00 h and 16:00 h. Similar methods have been used in other studies (Romero & Vasconcellos-Neto 2004, 2005a). At Monte Verde, plants from the forest ($n = 633$) and from the mountain top ($n = 529$) were inspected along two random 150 m \times 5 m transects (one per site). We also inspected



Figures 1–2.—*Coryphasia* spp., chelicerae, endites and labium, ventral view. 1. *C. monteverde* new species; 2. *C. cardoso* new species. Scale bars = 0.5 mm.

the non-bromeliaceous plants on the inselberg at Rio de Janeiro ($n = 500$) and in the restinga at Ilha do Cardoso ($n = 320$) along randomly located transects of $150 \text{ m} \times 5 \text{ m}$ and $70 \text{ m} \times 10 \text{ m}$, respectively (one per site).

To determine whether the *Coryphasia* spp. inhabited larger plants, as do other bromeliad-dwelling jumping spiders (Romero & Vasconcellos-Neto 2004, 2005a,b), we sampled the first 70 rosettes of *Ae. distichantha* found, 40 of them unoccupied and 30 occupied by *Coryphasia monteверde* on the mountain top at Monte Verde. The same was done for *C. cardoso* at Rio de Janeiro, using 81 rosettes of *A. glaziouana* (40 unoccupied and 41 occupied by this species). We did not evaluate the preference of *C. cardoso* for bromeliads of different sizes at Ilha do Cardoso. The size (surface area) of each rosette of *Ae. distichantha* was estimated as the product of the width (at the base) \times length of a leaf from the median layer (node) multiplied by 0.5, since the leaves of this species have a roughly triangular shape. The surface area of *A. glaziouana* was estimated using the same procedure but, since the leaves of this bromeliad have a rectangular shape, the product of the length \times width was not multiplied by 0.5. The leaf area of each rosette was multiplied by the total number of green leaves so as to obtain an approximation of the total plant surface area. Only the bromeliads *Ae. distichantha* and *A. glaziouana* were used in these analyses because they were the most abundant at Monte Verde and Rio de Janeiro, respectively. The distribution of the relative frequencies of the rosette size classes available and those occupied by *Coryphasia* spp. were compared using the G-test in a contingency table (Sokal & Rohlf 1995).

To determine which bromeliad species were inhabited most by *C. monteверde* at Monte Verde, we inspected the first 62 individuals of *Ae. distichantha*, 111 of *N. innocentii* and 60 of *V. bituminosa* that were found in the forest, in a plot of $150 \text{ m} \times 20 \text{ m}$, and the first 70 individuals of *Ae. distichantha* on the mountain top, in a plot of $50 \text{ m} \times 30 \text{ m}$, to allow comparison between habitats. We also determined which bromeliad species were used most by *C. cardoso* in Rio de Janeiro by inspecting the first 268 individuals of *A. glaziouana* and 88 individuals of *N. cruenta* available on the inselberg, in a plot of $150 \text{ m} \times 20 \text{ m}$. The use of bromeliad species by *C.*

cardoso at Ilha do Cardoso was assessed by inspecting 166 individuals of *Q. arvensis*, 48 individuals of *A. nudicaulis* and 55 individuals of *V. carinata* available in the restinga, along a $70 \text{ m} \times 10 \text{ m}$ transect. For each bromeliad inspected, we recorded the absence/presence of the spiders. Among the bromeliads from Monte Verde forest and Ilha do Cardoso, *Ae. distichantha*, *V. bituminosa*, *Q. arvensis* and *V. carinata* showed terrestrial and epiphytic habits, whereas *N. innocentii* and *A. nudicaulis* were apparently only terrestrial and epiphytic, respectively. However, we examined only bromeliads that occurred on the ground and epiphytes up to 1.5 m tall. The bromeliads from Rio de Janeiro were all ground-dwellers.

We compared the occupancy of the spiders on different plant species by using a G-test. To calculate an expected value for the observed number of plants of a given bromeliad species occupied by spiders, we multiplied the proportion of occurrence (abundance) of this bromeliad species by the total number of bromeliads occupied (of all bromeliad species). This procedure was used because of the variable abundance of plants of each bromeliad species. The results were expressed as the percentage of bromeliads occupied [(number of bromeliads occupied/total number of bromeliads) $\times 100$]. The *P*-values for multiple comparisons of the frequency of spiders on different bromeliad species (at Monte Verde) were adjusted using the Bonferroni correction ($P = \alpha/n = 0.05/3 = 0.017$).

RESULTS

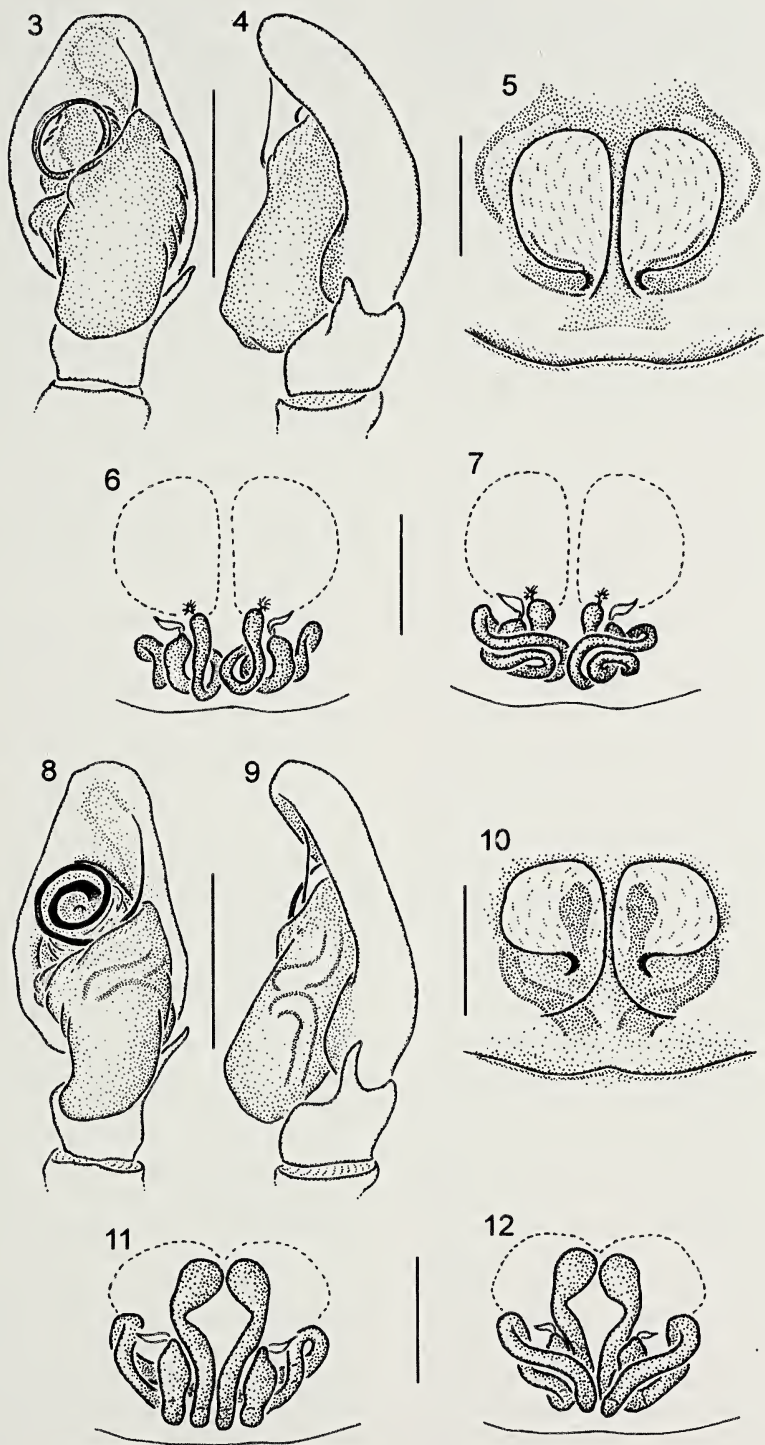
Coryphasia monteверde Santos & Romero new species Figs. 1, 3–7

Type material.—Male holotype from Monte Verde, state of Minas Gerais, Brazil, September 2003, G.Q. Romero coll., in IBSP 54541. Female paratype from the same locality, 9 August 2003, G.Q. Romero coll., in IBSP 54542.

Additional material examined.—BRAZIL: São Paulo: Jundiá, Serra do Japi, 26 June 2003, G.Q. Romero coll., 2♀ (IBSP 54543).

Etymology.—The species name is a noun in apposition taken from the type locality.

Diagnosis.—*Coryphasia monteверde* is



Figures 3–12.—*Coryphasia* spp. 3–7. *C. monteverde* new species: 3. Male palp, ventral view; 4. Male palp, lateral view; 5. Female epigynum, ventral view; 6. Female internal genitalia, dorsal view; 7. Female internal genitalia, ventral view. 8–12. *C. cardoso* new species: 8. Male palp, ventral view; 9. Male palp, lateral view; 10. Female epigynum, ventral view; 11. Female internal genitalia, dorsal view; 12. Female internal genitalia, ventral view. Scale bars = 0.5 mm.

similar to *C. melloleitaoi* Soares & Camargo 1948 and *C. fasciiventris* (Simon 1902) in their short posterior tegular lobe, which is the same width as the tegulum (Rinaldi & Avelino 2000: fig 14; Galiano 1963: figs. 5, 6). The males can be distinguished by the thin, flattened embolus, the large and anteriorly projected tegular ledge and the shorter retrolateral tibial apophysis (Figs. 3, 4). This species differs from *C. nigriventris* Mello-Leitão 1947 (Edwards et al. 2005: figs. 25–28) and *C. nuptialis* Bauab Vianna 1986 (figs. 12–14) by the embolus with a shorter, non-coiled apical portion. *Coryphasia castaneipedis* Mello-Leitão 1947 differs from all other species of the genus, including those described here, by the smaller embolus and the terminal lobe of tegulum pointed prolaterally (Edwards et al. 2005: fig. 21). *Coryphasia artemioi* Bauab Vianna 1986 (fig. 5) is probably misplaced in the genus, and presents palpal morphology consistent with the diagnosis of *Asaphobelis* Simon, 1902 as proposed by Edwards et al. (2005:23–24). Finally, *C. furcata* Simon 1902 and *C. albibarbis* Simon 1902 are similar, and differ from the remaining species of the genus, by the strongly curved terminal lobe of tegulum (Galiano 1963: figs. 6, 14). Females can be distinguished from all other species of the genus by the large lateral atria of the epigynum (Fig. 5) and the long seminal receptacle close to the spermathecae, with an apical star-shaped structure (Figs. 6, 7). This species also differs from the remaining species of the genus in the absence of anterior pockets in the epigynal atria (*C. fasciiventris*, Galiano 1963: fig. 7), and by the spermathecae located posteriorly to the epigynal atria, and not in their anterior half (*C. albibarbis*, Galiano 1963: fig. 16; *C. melloleitaoi*, Rinaldi & Avelino 2000: figs. 7, 8; *C. artemioi* and *C. nuptialis*, Bauab Vianna 1986: figs. 8, 16, respectively).

Description.—*Male (holotype)*: Carapace dark-brown, with black, pillose margins. Ocular area black, with long, semierect setae. Clypeus light brown, chelicerae red-brown, granulated, with apex of paturon and fangs orange. Labium and endites dusky, sternum yellow, covered with long hairs. Palps dusky. Legs I–II dusky, III–IV brown. Tarsus II–IV yellow. Legs I and II more robust than legs III and IV. Opisthosoma dusky, with a dorsal median yellow band with dark chevrons on the posterior half. Spinnerets gray, dusky lat-

erally. Total length 9.2. Carapace 4.2 long, 3.5 wide. Tibia I length 3.0, II 2.0, III 1.9, IV 2.1. Abdomen 5.0 long, 2.9 wide. Tegulum elliptic, with interior ducts barely visible.

Female (paratype): Carapace black, pillose, with a median red-brown band on anterior half of *pars thoracica*. Ocular area iridescent, with long hairs. Clypeus, chelicerae, labium and endites black, paturon granulated. Sternum red-brown, pillose, black in anterior lateral corners. Palps dark-brown. Leg I dark-brown, II–IV red-brown, coxae of all legs golden-yellow. Opisthosoma as in the male, without posterior chevrons. Spinnerets red-brown, darker laterally. Total length 10.4. Carapace 4.4 long, 3.6 wide. Tibia I length 2.1, II 1.6, III 1.8, IV 2.1. Abdomen 6.0 long, 3.8 wide. Internal genitalia with long, convoluted ducts, a pair of paramedian spermathecae with apical fertilization ducts and a pair of seminal receptacles (Figs. 6, 7).

Variation.—Females, total length 9.3–10.4, carapace width 3.3–3.6 ($n = 3$).

Distribution.—Known only from two mountain forest areas in southeastern Brazil.

Coryphasia cardoso Santos & Romero
new species
Figs. 2, 8–12

Type material.—Male holotype and two female paratypes from Parque Estadual da Ilha do Cardoso, Cananéia, state of São Paulo, Brazil, 16 April 2005, G.Q. Romero coll., respectively in IBSP 54538 and IBSP 54539.

Additional material examined.—BRAZIL: *Rio de Janeiro*: Rio de Janeiro, Sugar Loaf mountain (Pão de Açúcar), 30 December 2002, E. Wienkoski coll., 1♂ 2♀ 1 juv. (IBSP 24240).

Etymology.—The species name is a noun in apposition taken from the type locality.

Diagnosis.—*Coryphasia cardoso* males share with *C. albibarbis* Simon 1902 and *C. furcata* Simon 1902 a large, curved posterior tegular lobe (Galiano 1963: figs. 6, 14), but can be distinguished from both species by the longer embolus, which circles the base twice, the posterior tegular lobe which has a gentler curvature, and the ovoid apex of the cymbium (Fig. 8). Females are similar to *C. albibarbis* in their long seminal receptacle that is visible by transparency through the lateral atria of the epigynum (Galiano 1963: fig. 16), but differ from this species by the smaller atria (Fig. 10).

For more details on other species of the genus, see *C. monteverde* diagnosis.

Description.—*Male (holotype)*: Carapace dark-brown, pillose. *Pars thoracica* with a butterfly-shaped median red spot covered with white hairs. Ocular area black, with white hairs laterally and covered with long, semi-erect setae. Clypeus dusky, with a marginal fringe of white hairs. Chelicerae, labium and endites dark-brown, paturon granulated. Sternum gold-yellow, pillose, with marginal long hairs. Palps dark-brown. Leg I robust, dark-brown, II–IV red-brown, tarsus IV and apical half of metatarsus III–IV creamy. Opisthosoma creamy, with lateral dusky bands and posterior dusky chevrons. Sides black, venter creamy, with three longitudinal median dark stripes from epigastric furrow to spinnerets. Spinnerets creamy. Total length 6.4. Carapace 3.5 long, 2.8 wide. Tibia I length 1.8, II 1.6, III 1.6, IV 1.9. Abdomen 2.7 long, 1.8 wide. Tegulum long, gently curved prolaterally at the terminal lobe, with internal ducts visible by transparency (Figs. 8, 9).

Female (paratype): Color and hair covering as in the male, except for the following. Sternum red-brown. Coxae II red-brown, III–IV creamy. Total length 7.4. Carapace 3.5 long, 2.8 wide. Tibia I length 1.7, II 1.4, III 1.5, IV 2.0. Opisthosoma 4.0 long, 2.6 wide. Internal genitalia with lateral, convoluted copulatory ducts; paramedian spermathecae with apical fertilization ducts and a pair of median, long and apically spherical seminal receptacles (Figs. 11, 12).

Variation.—Females, total length 6.6–9.4, carapace width 2.8–3.3 ($n = 4$). Male from Rio de Janeiro (see below) with total length of 10.0 and carapace width of 3.8. Specimens from Rio de Janeiro are generally larger and darker than those from the type locality, and do not have the butterfly-shaped spot on the carapace.

Distribution.—Known only from two mountain forest and restinga areas in southeastern Brazil.

Association with bromeliads.—*Coryphasia* spp. did not inhabit non-bromeliad plants at Monte Verde and Ilha do Cardoso. However, in Rio de Janeiro, five individuals of *C. cardoso* were found on five non-bromeliad plants. In these cases, the plants occupied were shrubby and located up to 30 cm above thickets of the bromeliad *A. glaziouana*.

Coryphasia monteverde occurred non-randomly on individuals of *Ae. distichantha* of different sizes (surface area) at Monte Verde, with the highest frequency on larger bromeliads (contingency table, $G = 15.8$, $df = 5$, $P = 0.007$, Fig. 13). In contrast, in Rio de Janeiro the frequency of *C. cardoso* among individuals of *A. glaziouana* of varying size classes did not differ statistically (Fig. 13; contingency table, $G = 10.0$, $df = 5$, $P = 0.075$). The surface area of *A. glaziouana* was larger than that of *Ae. distichantha* (*A. glaziouana*: 9254 ± 670 cm², $n = 81$; *Ae. distichantha*: 902 ± 56 cm², $n = 70$; Mann-Whitney test, $U = 2524$, $P < 0.001$; see also Table 1).

In the forest at Monte Verde, *C. monteverde* used the available bromeliads non-randomly ($G = 24.14$, $df = 2$, $P < 0.001$, Fig. 14), and occurred at a higher frequency on *Ae. distichantha* compared to *N. innocentii* ($G = 24.13$, $df = 1$, $P < 0.001$) and on *V. bituminosa* relative to *N. innocentii* ($G = 7.70$, $df = 1$, $P = 0.005$). The frequency of *C. monteverde* between individuals of *Ae. distichantha* and of *V. bituminosa* did not differ statistically ($G = 3.65$, $df = 1$, $P = 0.056$). In this habitat, *V. bituminosa* was the largest bromeliad species (Table 1). This spider species was more common on *Ae. distichantha* from the mountain top (i.e., open area) than on individuals of this bromeliad species from forest ($G = 5.42$, $df = 1$, $P = 0.020$, Fig. 14), despite the smaller size of *Ae. distichantha* from the open area compared to that of forest specimens (mountain top: 902 ± 56 cm², $n = 70$; forest: 1446 ± 178 cm², $n = 17$; Mann-Whitney test, $U = 1022$, $P = 0.003$). In Rio de Janeiro, *C. cardoso* was more common on *A. glaziouana* than on *N. cruenta* ($G = 30.22$, $df = 1$, $P < 0.001$, Fig. 14). At this site, *A. glaziouana* was larger than *N. cruenta* (Table 1). At Ilha do Cardoso, the frequency of *C. cardoso* did not vary between the bromeliads *V. carinata* and *Q. arvensis* ($G = 2.33$, $df = 1$, $P = 0.127$), and this spider did not occur on *A. nudicaulis* (Fig. 14). The latter bromeliad was the smallest of those found at Ilha do Cardoso (Table 1). In Serra do Japi, we have monitored a population of *C. monteverde* established in a thicket of *B. antiacantha* for > 5 yr.

At Monte Verde, we found six and three egg sacs of *C. monteverde* on the leaves of *Ae. distichantha* in the forest and on the

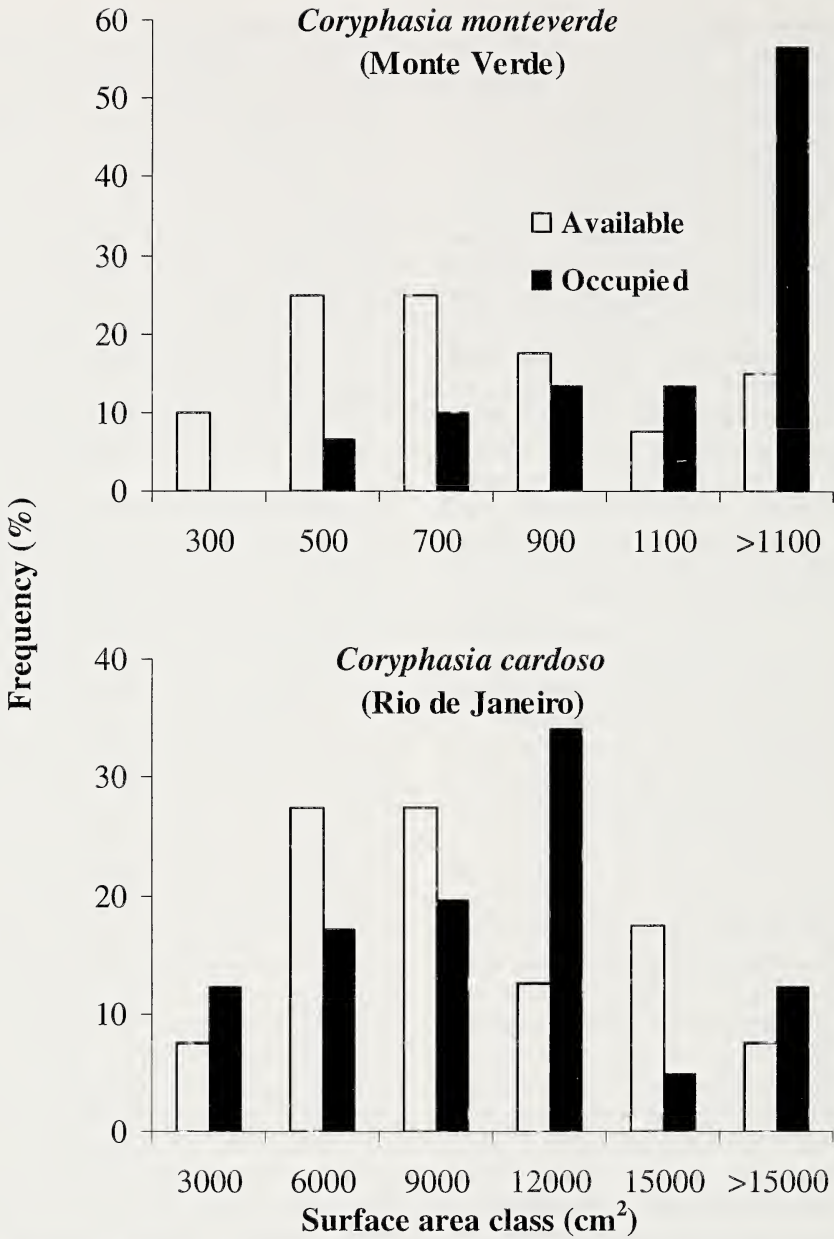


Figure 13.—Relative frequency of different size classes of *Aechmea distichantha* (from Monte Verde) and *Alcantarea glaziouana* (from Rio de Janeiro) occupied by *C. monteverde* ($n = 30$) and *C. cardoso* ($n = 41$) (black bars), respectively, compared to the total availability of these bromeliads (*A. distichantha*: $n = 70$; *A. glaziouana*: $n = 81$) (open bars).

mountain top, respectively. In Serra do Japi, we found one egg sac of this spider species on *B. antiacantha*. In Rio de Janeiro, we found five egg sacs of *C. cardoso* on *A. glaziouana*. No egg sacs were found on the bromeliads at Ilha do Cardoso.

Generally, when approached by an observer

trying to capture them, the two *Coryphasia* species climbed down a leaf to submerge in the water of tank bromeliads (e.g., *Ae. distichantha* and *A. glaziouana*). The spiders remained submerged for more than three minutes and were apparently surrounded by an air bubble. We have not observed this submer-

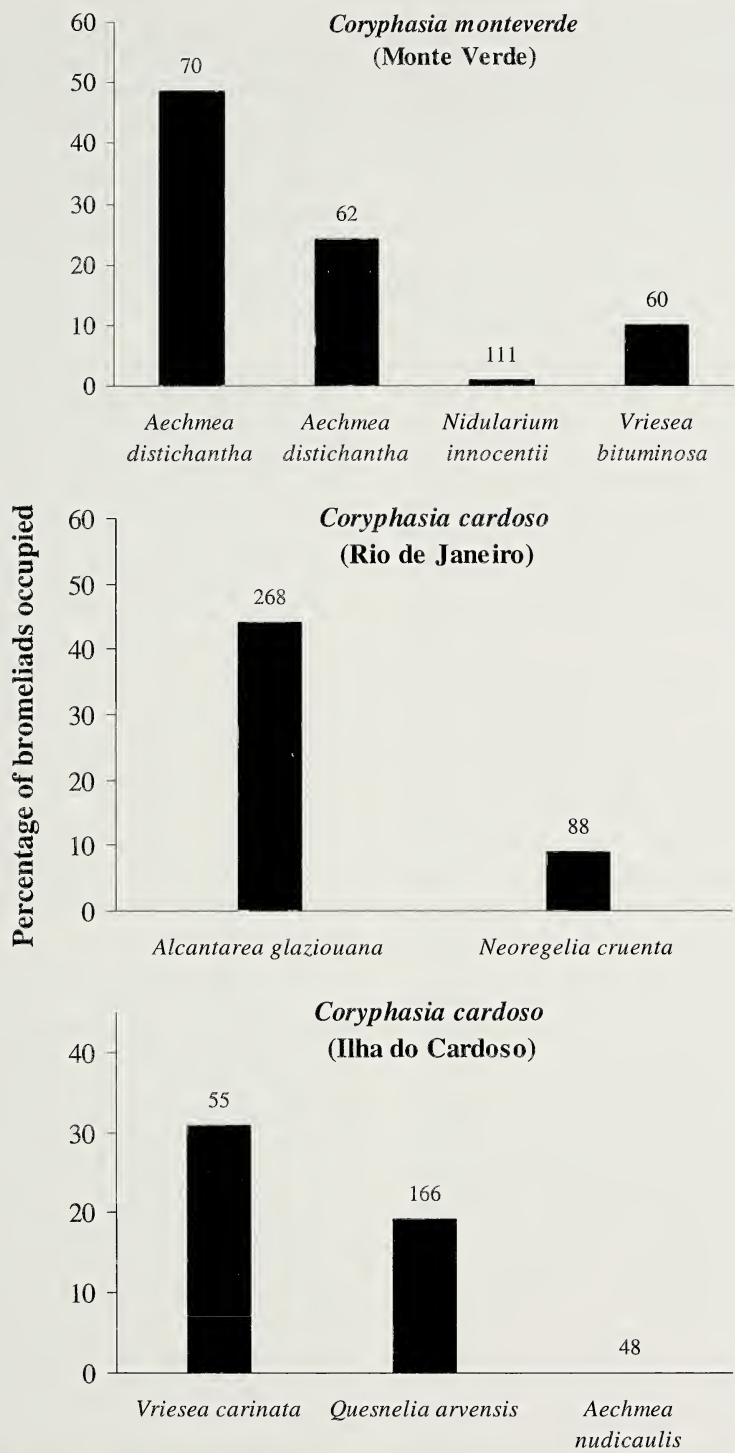


Figure 14.—Percentage of bromeliad species occupied by *C. monteverde* in the inselberg (first bar to the left) and forest (remaining three bars to the right) at Monte Verde, and by *C. cardoso* in the inselberg at Rio de Janeiro and restinga at Ilha do Cardoso. The number of plants inspected is indicated above the bars.

gence behavior in *C. cardoso* from Ilha do Cardoso. When on bromeliads that do not form phytotelmata (e.g., *B. antiacantha* from Serra do Japi), *C. monteverde* individuals quickly fled to peripheral leaves and buried themselves in the bromeliad rosette.

DISCUSSION

Our results indicate that *C. monteverde* and *C. cardoso* were specifically associated with bromeliads since they were rarely found on non-bromeliad plants. Moreover, these species inhabited bromeliads in different geographic regions, indicating a strong, specific relationship between these spiders and the Bromeliaceae. Bromeliads may be a suitable microhabitat for salticids because their leaves form a complex tridimensional architecture that allows adult spiders to forage and to shelter from predators (Romero & Vasconcellos-Neto 2005a,c). Moreover, plants in rosette shape may be good sites for spiders to lay eggs and as nurseries for spiderlings (Santos et al. 2002; Romero & Vasconcellos-Neto 2004, 2005a,c). In addition, since several bromeliad-dwelling spiders live in open areas (e.g., Santos et al. 2002; Dias & Brescovit 2003, 2004; Romero & Vasconcellos-Neto 2004, 2005a,b; Romero 2006), where the ground (e.g., sandy or rocky habitats) is generally hot during the day, bromeliads may provide shelter against high temperatures. We observed that the ground temperature on the inselberg at Monte Verde reached 50° C during the day (15:00 h), while among the bromeliad leaves and in the phytotelmata the temperature was 27° C and 22° C, respectively. Hence, the phytotelmata appear to function as a thermoregulatory mechanism for the bromeliads and indirectly provide a suitable microclimate for the spiders (see also Dias & Brescovit 2004).

Coryphasia monteverde inhabited the larger rosettes of *Ae. distichantha* at Monte Verde, which suggested that these spiders may actively select their microhabitats based on host plant size. Romero & Vasconcellos-Neto (2004) reported that another bromeliad-dwelling salticid, *E. nativo*, had a similar microspatial distribution on two bromeliad species, possibly because larger plants have a higher probability of being visited by insects as a result of their large surface area. However, in Rio de Janeiro, *C. cardoso* apparently did not discriminate the rosettes of *A. glaziouana* by

their size, perhaps because the detection of variation in rosette size among such large bromeliads (this species is much larger than *Ae. distichantha*) may be difficult or unnecessary for *C. cardoso*.

In the forest at Monte Verde, *C. monteverde* occurred at a higher frequency on *Ae. distichantha* and *V. bituminosa* than on *N. innocentii*, while in Rio de Janeiro, *C. cardoso* occurred at a higher frequency on *A. glaziouana* than on *N. cruenta*. *Vriesea bituminosa* and *A. glaziouana* were the largest bromeliads available in each region, and the spiders may have selected these plants because of their size. Although *Ae. distichantha* is a small bromeliad, it was the only one in the forest that had conspicuous spines at the edges of its leaves. These spines may provide protection against small vertebrates, as suggested by Romero & Vasconcellos-Neto (2005a,c) for other salticid-bromeliad systems. *Coryphasia cardoso* also inhabited the largest bromeliads, *V. carinata* and *Q. arvensis*. However, these spiders did not select plants with spines at their leaf margins in either of their areas of occurrence. Hence, this morphological trait in the plants from Rio de Janeiro (e.g., *N. cruenta*) and Ilha do Cardoso (e.g., *Q. arvensis*) may have no protective function for this *Coryphasia* species. Alternatively, this spider species may not select host plants that have spines on their leaf margins. *Coryphasia cardoso* did not occur on *A. nudicaulis* at Ilha do Cardoso. This bromeliad species, which was the smallest of the bromeliads available at this site, had leaves that were strongly clustered to form a tube-like rosette. This architecture may be unsuitable for active hunters such as Salticidae spiders that generally live and forage in tri-dimensional, open microhabitats (Romero & Vasconcellos-Neto 2004, 2005c). Alternatively, *C. cardoso* may avoid competition with and/or predation by females of the harvestman *Bourguyia albiornata* Mello-Leitão 1923, which frequently use *A. nudicaulis* as an oviposition site at Ilha do Cardoso (Machado & Oliveira 2002).

Coryphasia monteverde occurred more frequently on mountain top bromeliads, where the ground is rocky and trees are scarce, than on forest-dwelling rosettes. Romero & Vasconcellos-Neto (2005a) reported a similar dispersion pattern for *P. chapoda*, which was more common on rosettes of *B. balansae* from

grasslands (open areas) than on rosettes from forest understories. Romero & Vasconcellos-Neto (2005c) demonstrated that fallen dry leaves from forest trees blocked the base (center) of *B. balansae* and effectively prevented the spiders' access to shelter and rest sites. In the present study, several forest-dwelling bromeliads had many dry leaves from trees in their rosettes, and this may have prevented *C. monteverde* from taking shelter in the water source (phytotelmata).

The habit of the two *Coryphasia* spp. of submerging in the water of phytotelmata may be an anti-predator adaptation for living on bromeliads. Similar submergence behavior has been recorded for two other bromeliad-dwelling jumping spiders, *Eustiromastix nativo* and *Psecas* sp. (Romero & Vasconcellos-Neto, unpublished data). These results suggest convergent behavior among these jumping spiders for living on tank-bromeliads.

In conclusion, *C. monteverde* and *C. cardoso* were specifically associated with bromeliads in different geographic regions and inhabited the larger bromeliads among those available. These spiders submerged in water of the bromeliad phytotelmata, as do other bromeliad-living jumping spiders, possibly as a protective adaptation for inhabiting tank bromeliads.

ACKNOWLEDGMENTS

The authors thank G.B. Edwards, J.R. Trigo, M.O. Gonzaga, C. Viera, P.I. Prado, P.S. Oliveira and F.R. Scarano for reviewing the first draft of the manuscript. G.B. Edwards and G. Ruiz contributed with taxonomic discussions regarding *Coryphasia* species, L. Meireles and G. Martinelli identified the bromeliads, and I. Lewinsohn helped with the data collection. G.Q. Romero and A.J. Santos were supported by research grants from Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP, grant no. 01/04610-0 to G.Q.R. and 03/04868-3 to A.J.S.). J. Vasconcellos-Neto was supported by a grant from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, grant no. 300539/94-0). This paper is part of the BIOTA/FAPESP—The Biodiversity Virtual Institute Program (<www.biota.org.br> proc. 99/05446-8).

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Manuscript received 29 May 2006, revised 16 October 2006.

SHORT COMMUNICATION

CRITICAL THERMAL MAXIMUM OF THE GREEN LYNX SPIDER, *PEUCETIA VIRIDANS* (ARANEAE, OXYOPIDAE)

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ABSTRACT. The critical thermal maximum (CTMax) of *Peucetia viridans* Hentz 1832 adult spiders was determined in the laboratory. Mean temperature at death was higher for gravid spiders (49.4° C) than for postparturient females (47.2° C) and males (46.9° C). Painted copper spider models placed in the environment to examine available temperatures predicted that spider body temperatures would rarely exceed 40° C thus making it unlikely for *P. viridans* to naturally reach CTMax, at least in the climate of central Tennessee.

Keywords: Temperature, thermal tolerance

The range of thermal tolerances in ectothermic animals is important for better understanding the limitations of an animal's thermal ecology and behavior. An organism's upper and lower thermal limits can influence many aspects of life, including foraging, habitat selection, mating, and development (Angilletta et al. 2002). More specifically in spiders, those thermal limits could be useful in evaluating the suitability of foraging and nest-site habitats, especially in those species where the female remains at her nest guarding her egg sac. As organisms approach their thermal limits, negative physiological affects are typically observed, potentially culminating in death. The critical thermal maximum (CTMax) is a standard measure to evaluate the thermal requirements and physiology in organisms because the behavioral and physiological responses are the same across a wide diversity of taxa (Lutterschmidt & Hutchison 1997a). The commonly used dynamic method gradually increases the temperature until an end-point is reached (Lutterschmidt & Hutchison 1997b). Cowles & Bogert (1944) first introduced this method and the CTMax was defined as "the thermal point at which locomotor activity becomes disorganized and the animal loses its ability to escape from conditions that will promptly lead to its death."

The temperature change in the dynamic method must be gradual enough to allow the core temperature of individuals to equilibrate to the test tem-

perature without a significant time lag (Hutchison 1961), with heating rates of 0.5 to 1.5° C per min often being used (Lutterschmidt & Hutchison 1997b). Although various measuring points (e.g., loss of the righting response, sudden onset of muscular spasms, and death (Lutterschmidt & Hutchison 1997a, 1997b)) have been used to describe the CTMax, Lutterschmidt & Hutchison (1997a) support the use of onset of muscular spasms as the CTMax. However, the studies they reviewed primarily used ectothermic vertebrates. Muscular spasms in small invertebrates may be difficult to observe, thus other means (e.g., temperature at the point of thermal discomfort or temperature at death) may be necessary to determine the thermal limits.

The thermal biology of few spider species have thus far been studied (Humphreys 1987; Schmalhofer 1999), which has limited our knowledge of thermal tolerances and preferences associated with differing microhabitats. The CTMax has been described in a few species including *Loxosceles intermedia* Mello-Leitão 1934 and *L. laeta* Nicolet 1849 in Brazil (Fischer & Vasconcellos-Neto 2003), a number of dune-living spiders in Sweden (Almquist 1970), a riparian spider (Devito & Formanowicz 2003), an orb-weaving spider (Tolbert 1979), and two crab spiders (Schmalhofer 1999). In Schmalhofer's study *Misumenops asperatus* Hentz 1847 matured in the spring and *Misumenoides formosipes* Walckenaer 1837 in the summer. As predicted, the summer maturing spider experiencing higher temperatures was found to have a higher CTMax (Schmalhofer 1999). Also, crab spiders hunting on flowers exposed to warm temperatures had a higher CTMax, which presumably allowed them to forage

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Table 1.—CTMax determination temperatures (mean \pm SD) and range for *P. viridans*.

Adult Category	Thermal Discomfort Point ($^{\circ}$ C)	Onset of Muscular Spasms ($^{\circ}$ C)	Temperature at Death ($^{\circ}$ C)
Male ($n = 3$)	40.3 \pm 3.1 (38.3–43.9)	43.0 \pm 2.9 (39.8–45.5)	46.9 \pm 0.2 (46.8–47.1)
Gravid Female ($n = 3$)	41.0 \pm 1.4 (39.5–42.1)	43.1 \pm 1.2 (42.1–42.8)	49.4 \pm 0.9 (48.6–50.3)
Postparturient Female ($n = 4$)	40.0 \pm 2.3 (38.5–43.4)	42.4 \pm 1.6 (40.6–44.0)	47.2 \pm 0.4 (46.8–47.8)

more freely on pollinating insects (Schmalhofer 1999).

The green lynx spider, *Peucetia viridans* Hentz 1832, is an ambush predator that hunts near the top of flowering herbaceous plants and feeds on pollinating insects in the southern United States and Mexico (Turner 1979; Willey & Adler 1989; Arango et al. 2000). Males and gravid females can be found on flowering vegetation in field habitats during the summer and early autumn. Males die soon after mating in early August and gravid females then lay an egg sac near the top of vegetation. Postparturient females remain with and protect their egg sac until spiderlings emerge and disperse (Fink 1987). Without females to protect the egg sac, ant predation and dislodgement commonly occur (Fink 1986, 1987; Hanna & Cobb 2006). Females attending egg sacs are exposed to the same ambient temperatures as their egg sacs (Hanna & Cobb 2006). These temperatures may be beneficial for egg development, but potentially could reach harmful levels for an adult spider. Understanding the CTMax of adult *P. viridans* could be useful in evaluating how suitable foraging and nest-site habitats are for guarding females.

The purpose of this study was to test whether gravid *P. viridans* have a higher thermal tolerance than postparturient female and male spiders. Because gravid females are generally located at more exposed sites on vegetation, we hypothesized that they may have a higher thermal tolerance. To obtain natural thermal conditions that spiders could be exposed to during the egg sac incubation period, we placed physical spider models in the field to measure potential spider temperatures.

Using the dynamic method, the CTMax was measured for three mature males, three gravid females, and four postparturient females. We collected postparturient females from the field within 48 h of producing an egg sac in September 2004. Spiders were collected from Rutherford County, Tennessee and voucher specimens have been deposited in the entomology collection at Middle Tennessee State University. Adult spiders were housed in a laboratory at 21.5 $^{\circ}$ C for 24 h prior to testing. For testing, we moved spiders to 5 \times 8 cm cylinders covered with cheese cloth and placed them in an environmental chamber (Percival I-36LL). Trials

initially started at 25 $^{\circ}$ C, increased at increments of 0.2 $^{\circ}$ C every 3 min, and could reach 50 $^{\circ}$ C. Three thermal end-points to the trials were measured. The first temperature recorded was the thermal discomfort point, or the point at which the spiders initiate rapid movement around their enclosure. The second temperature recorded was when the onset of spasms occurred. The third temperature recorded was the temperature at death, indicated by cessation of movement. To record these measurements, we positioned spiders within the chamber so that they could be video recorded via a chamber ventilation hole. One-way ANOVAs and Student-Newman-Keuls post hoc tests were used to compare the CTMax measurements.

For the test spiders, the thermal discomfort point, the temperature at the onset of spasms and the temperature at death were recorded (Table 1). No significant differences between males, gravid females, or postpartum females were observed for the thermal discomfort point ($F_{2,7} = 0.162$, $P = 0.854$) or the temperature at the onset of muscular spasms ($F_{2,7} = 0.137$, $P = 0.874$). However, gravid females did have a significantly higher temperature at death ($F_{2,7} = 19.34$, $P = 0.001$), than either males or postpartum females.

To determine potential temperatures that *P. viridans* may experience in the field, we placed physical spider models in typical locations where spiders were observed during the egg-laying season. We constructed spider models out of a hollow copper tube (2 mm diam., 20 mm long) for the body, and 20 ga copper wire for the legs. One end of the model was sealed with a waterproof sealant (i.e., caulk), and a 30 ga type T thermocouple wire was sealed inside the other end (Fig. 1). The thermocouple wire was measured with a multi-channel datalogger (Campbell Scientific, Inc. CR23x). Initially we placed the following models outdoors: models spray-painted black, neon green, jade, yellow, pebble, and white, along with two recently sacrificed gravid females and one male spider, on a 50 cm \times 50 cm white styrofoam tile (used to reduce convective heating from the ground). Body temperatures of sacrificed spiders were measured using a thermocouple wire inserted in their abdomen. We monitored both spiders and models for 80 min, and purposefully moved them into and out of bright sun

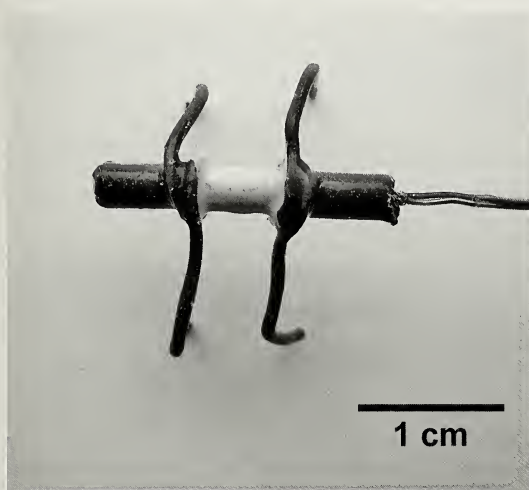


Figure 1.—A painted spider model with a thermocouple wire attached.

and full shade to determine which painted model was most thermally similar to real spiders.

Graphical comparison of the painted spider models to actual spiders revealed the neon green model was 1–2° C warmer, while the pebble green model was 1–2° C cooler. Therefore, we painted a model with the distal thirds neon green and the middle third pebble and again compared the model to two recently sacrificed female spiders. The banded model differed on average by 0.08° C from the real spiders (Fig. 2) ($r^2 = 0.981$, $P < 0.001$), with no significant differences between the spider and the model (paired $t = 0.705$, $P = 0.482$). Therefore, our model spiders accurately predicted the temperature of real spiders, including times of heating and cooling, which made it possible to predict spider body temperature without disturbing or harming real spiders.

We placed three banded model spiders in the field at positions where real spiders were typically observed and recorded temperatures at 10 min intervals for 50 days beginning 7 September 2004. All three models were 75 cm above the ground; one placed on a south-facing vertical stem, a second placed on top of a goldenrod (*Solidago nemoralis*) inflorescence, and a third placed under the inflorescence of *S. nemoralis* (common location of egg sacs).

In the field, the warmest spider model was on the south-facing stem at 75 cm, with the warmest temperature recorded being 39.3° C. The warmest temperature recorded for the other models was 35.2° C (under the goldenrod inflorescence) and 36.5° C (exposed on the inflorescence). The maximum difference in temperature between different models during the day was 10.8° C on 17 September, when the temperature on the south-facing stem was 39.2° C and the model below the inflorescence was 28.4°

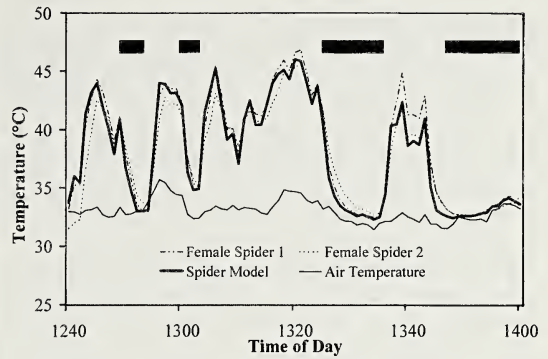


Figure 2.—Temperature comparisons for a painted spider model and two female green lynx spiders on 27 August 2004. Shaded air temperature was measured near the models. Bars indicate when spiders and models were moved into full shade.

C. While model placement greatly influenced predicted temperatures, differences potentially could be even larger if the spider selected plants with more vegetative growth and consequently more shade.

Gravid female *P. viridans* are often found in open field habitats on flowering vegetation foraging during the summer when air temperatures can be quite warm (i.e., August). Withstanding warmer temperatures is beneficial for gravid females that are foraging heavily before expending energy producing an egg sac. This provides gravid females the benefit of foraging in places or during times when it would potentially be too warm for males or non-gravid females. Male *P. viridans* die soon after mating, and are rarely observed in the field when females begin laying their egg sacs. Therefore, male *P. viridans* are generally not foraging during the warmest part of summer, but rather they spend more time seeking a mate, moving between different microclimates. Postparturient females occurred on or near their egg sacs and were infrequently found with prey. In addition, postparturient females are rarely found exposed on inflorescences. Notably, postparturient females have a lower CTMax than gravid females, but it is still 8° C higher than the warmest temperature recorded by a model spider in the field, meaning temperatures in central Tennessee should not harm or stress *P. viridans* while guarding their egg sacs.

Although the field temperatures in this study did not approach the maximal thermal limitations for *P. viridans*, it should be noted that the spider models were monitored during September and October when postparturient females are prevalent. In central Tennessee, temperatures occasionally become warm enough in late summer to reach CTMax, as indicated by our spider-model calibration in August (Fig. 2). These are the temperatures gravid females

would most likely be experiencing and may account for their higher temperature at death measurement (Table 1). It should also be noted that the summer of 2004 in central Tennessee was not unusually warm and *P. viridans* populations further south in their range would probably be exposed to higher temperatures.

Because of the high surface to volume ratio in *P. viridans* body dimensions, low thermal inertia is expected giving *P. viridans* the ability to heat and cool quickly. Using data from the initial paint matching test, we calculated the heating and cooling rates for three sessions using one male and two female spiders. Heating rates did not differ from cooling rates and the mean rate of change for the male spider was 3.1° C per min ($n = 6$ sessions) and for females was 2.6° C per min ($n = 12$ sessions). Combined heating/cooling rate for all three spiders was 2.8° C per min.

Such a low thermal inertia makes it likely that microhabitat variation allows spiders to simply make short movements to a cooler location if CTMax is approached. Although geographic variation and plasticity of CTMax in spiders remains to be tested, this implies, in general, that the likelihood that small spiders would encounter lethal body temperatures is low and that only in extreme environments with little thermal microhabitat differences would a spider species be at risk of overheating. However, implications for species behaviorally limited by factors such as web or egg sac placement risks would remain.

ACKNOWLEDGMENTS

We thank the Tennessee Department of Environment and Conservation and The Nature Conservancy for allowing us to collect and observe spiders on their property. Funding was provided by Middle Tennessee State University's (MTSU) Faculty Research and Creative Activity Committee and Department of Biology. Animal protocols were approved by MTSU's Institutional Animal Care and Use Committee.

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Manuscript received 9 January 2006, revised 14 July 2006.

SHORT COMMUNICATION

A NEW SPECIES OF *DRASSYLLUS* (ARANEAE, GNAPHOSIDAE) FROM WEST TEXAS

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ABSTRACT. A new species, *Drassyllus broussardi*, is described from Presidio County, West Texas, USA. The species belongs to the *insularis* group but has a distinctively elongated embolus in males and concomitantly elongated copulatory ducts in females.

Keywords: Zelotinae, Texas, Presidio County, *insularis* group

The zelotine gnaphosid genus *Drassyllus* includes a substantial fraction of the North American ground spider fauna; the 61 currently known New World species, found from southern Canada to southern Mexico, have been assigned to eight species groups (Platnick & Shadab 1982; Platnick 1984; Platnick & Corey 1989).

Midwestern State University, at Wichita Falls, Texas, recently received a donation of land straddling Presidio and Brewster Counties in West Texas for research aimed at understanding the operation of a desert ecosystem. This parcel, the Dalquest Research Site, is near the Big Bend Ranch State Park and provides a valuable opportunity to study a relatively undisturbed portion of Chihuahuan desert. Under the direction of the second author, a survey of the spider fauna of the Dalquest Research Site was carried out by Mr. Greg Broussard as part of his M.S. degree research. Unsurprisingly, a number of unusual and relatively unfamiliar spiders occur at the site, and we report here on one of them: a gnaphosid ground spider belonging to the *insularis* group of *Drassyllus*. The largest of the eight species groups, the *insularis* group includes taxa primarily from the western United States, along with many Mexican endemics (Platnick & Shadab 1982). The group is not well known, especially in Mexico, where many of the species are so far identified only from females. Nevertheless, the species found at the Dalquest site differs clearly from all the previously known taxa, and is here newly described.

We thank Dr. Mohammad Shadab of the American Museum of Natural History for his work on the illustrations. Specimens are housed in the collections of the American Museum of Natural History,

New York (AMNH) and Midwestern State University, Wichita Falls, Texas (MWSU).

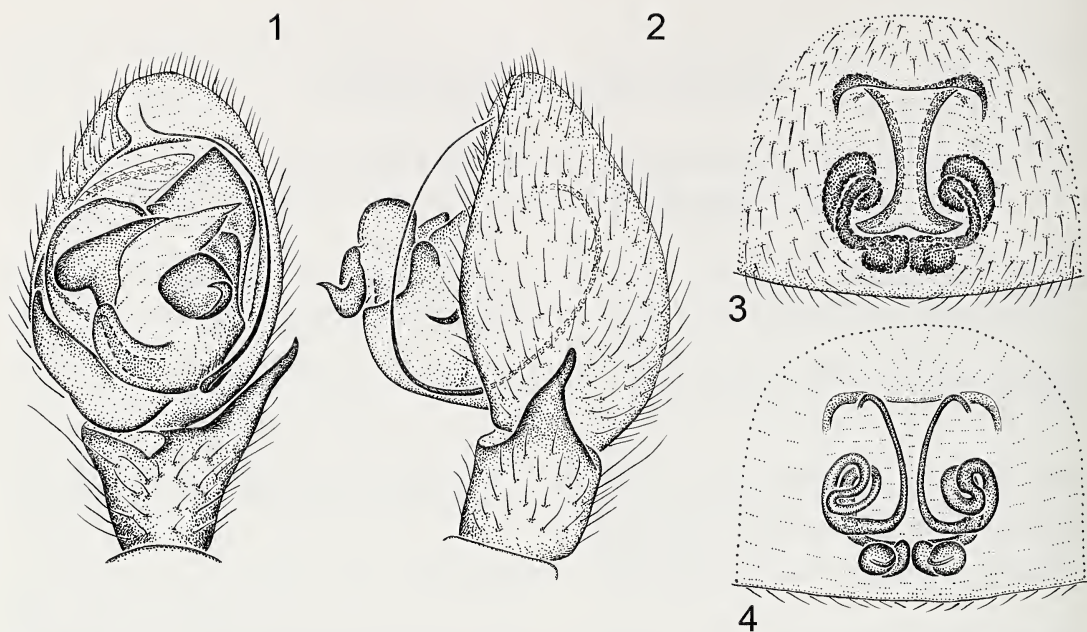
Family Gnaphosidae Pocock 1898
Genus *Drassyllus* Chamberlin 1922

Type species.—*Drassyllus fallens* Chamberlin 1922, by original designation.

Drassyllus broussardi new species
Figs. 1–4

Types.—Holotype male taken in uncovered, dry pitfall trap at an elevation of 1,267 m at the Dalquest Research Site, 29°33.41'N, 103°47.65'W, Presidio County, Texas, USA, 8 August 2005, N. Horner, J. Rogers (AMNH). Allotype female taken in covered, propylene glycol pitfall trap at the same locality 22 July–7 August 2005, N. Horner (AMNH).

Other material examined.—USA: Texas: Presidio County: 7 ♂, Dalquest Research Site, 29°33.41'N, 103°47.65'W, elev. 1267 m, 6–19 August 2004, pitfalls, N. Horner (AMNH); 4 ♂, same location, 20 August–4 September 2004, pitfalls, N. Horner (AMNH); 5 ♂, same location, 22 July–7 August 2005, covered glycol pitfalls, N. Horner (AMNH); 2 ♂, same location, 7 August 2005, uncovered alcohol pitfalls, N. Horner (AMNH); 1 ♂, 1 ♀, same location, 8 August 2005, covered dry pitfalls, N. Horner, J. Rogers (MWSU); 1 ♀, same location, 9 August, 2005, uncovered dry pitfall, N. Horner, J. Rogers (AMNH); 3 ♂, same location, 11 August–10 September 2005, uncovered glycol pitfalls, N. Horner (AMNH); 2 ♂, 2 ♀, same location, same date, covered glycol pitfalls, N. Horner (AMNH).



Figures 1–4.—*Drassyllus broussardi*, new species: 1. Left male palp, ventral view; 2. Left male palp, retrolateral view; 3. Epigynum, ventral view; 4. Epigynum, dorsal view.

Etymology.—The specific name is a patronym in honor of Greg H. Broussard, in recognition of the many valuable specimens taken in his survey work at the type locality.

Diagnosis.—The pair of median extensions on the anterior epigynal ducts (Fig. 4) support the assignment of this species to the *insularis* group, as does the absence of stiff setae dorsally on the male palpal tibia. Males can easily be distinguished from those of all the other members of the group by their greatly elongated embolus, which occupies most of the retrolateral extent of the palpal bulb (Figs. 1, 2). As expected, females have concomitantly elongated copulatory ducts, the length of which is accommodated by lateral convolutions that are also unique (Figs. 3, 4). Measurements are expressed in mm.

Male (holotype).—Total length 2.02. Carapace 0.89 long, 0.67 wide. Femur II 0.55 long. Carapace light yellow, darkest anteriorly, rear of pars cephalica with dusky markings; abdominal dorsum dark gray, venter white; legs light yellow. Leg spination typical for genus except: femora I–IV p0-0-0, r0-0-0; patella III r0-0-0; tibiae III, IV p0-0-0, r0-0-0; metatarsi I–IV spineless. Terminal apophysis long, narrow, directed retrolaterally; embolus greatly elongated, making almost complete coil, dorsal half hidden inside cymbium (Fig. 1); retrolateral tibial apophysis triangular, distally narrowed, angled (Fig. 2).

Female (allotype).—Total length 2.24. Carapace 0.88 long, 0.66 wide. Femur II 0.56 long. Coloration as in male. Leg spination as in male except tibiae III, IV spineless. Anterior epigynal margin occupying full width of epigynum, with short posterolateral extensions (Fig. 3); epigynal ducts coiled laterally (Fig. 4).

Distribution.—Known only from Presidio County, West Texas, USA.

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Manuscript received 16 March 2006, revised 19 May 2006.

SHORT COMMUNICATION

PARENTAL CARE IN THE NEOTROPICAL HARVESTMAN *PHAREICRANAUS CALCARIFERUS* (OPILIONES, CRANAIDAE)

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ABSTRACT. Parental care in harvestmen may take several forms including egg hiding, egg guarding, egg transport and young guarding. In most species, one adult, usually the female, performs guarding of the young. From 9 July–3 August 2005, we made observations of parental care by adults of the Neotropical cranaid harvestman *Phareicranaus calcariferus* (Simon 1879) in northern and central Trinidad. Nine observations involved an adult female and young while three appeared to include both an adult female and male with young. The number of young present was inversely related to the size of the young, indicating that parental care in this species may occur over an extended period of time.

Keywords: Biparental care, young guarding, Trinidad

Parental care can be generally defined as any behavior performed by an adult that enhances the survival of its progeny (Trivers 1972). Selective pressures that are believed to contribute to the evolution of parental care in harvestmen include predation (ants), cannibalism, and fungal infection (Mora 1990). In Neotropical harvestmen (Opiliones, Laniatores), parental care may take several forms including egg burying, egg hiding, egg carrying, and the guarding of eggs and early hatched nymphs (Machado & Raimundo 2001). Egg burying or egg hiding occurs when eggs are oviposited in the soil, among the leaf litter or in bark crevices (Machado & Raimundo 2001; Willemart 2001). In a few species, eggs may be laid and subsequently covered with debris (Willemart 2001; Pereira et al. 2004). Egg and young guarding specifically refers to a form of parental care in which one or both parents actively protect the progeny. In the gonyleptid species *Acutisoma longipes* Roewer 1913, the guarding female remains with the brood, occasionally touches the eggs with the second pair of legs, and regularly inspects the periphery of the clutch (Machado & Oliveira 1998; Machado 2002).

In Neotropical harvestmen, maternal care has been observed in at least 22 species representing four families including the Cosmetidae (Goodnight & Goodnight 1976), Gonyleptidae (Machado & Raimundo 2001), Stignopsidae (Mitchell 1971), and

Cranaidae (Machado & Warfel 2006). Of these taxa, egg hiding as well as egg and early nymph guarding by the female has been most extensively studied in the Gonyleptidae (Machado & Raimundo 2001). In *A. longipes*, maternal care includes egg and young guarding and may continue for a period of 56–78 days (Machado & Oliveira 1998). In contrast, paternal care has been observed in relatively few species, although it is known to occur in the Assamiidae (Martens 1993), Gonyleptidae (Machado et al. 2004), Manaosbiidae (Mora 1990), Podoctidae (Martens 1993), and Triaenonychidae (Forster 1954). Paternal care may take the form of egg transport (Martens 1993) or egg/young guarding (Mora 1990; Martens 1993; Hara et al. 2003; Machado et al. 2004). Biparental care of eggs or young has not been previously reported. However, in *Goniosoma albiscriptum* Mello-Letão 1932 and *A. longipes*, males will assume parental care if the guarding female is removed (Machado & Oliveira 1998; Willemart & Gnaspini 2004).

This paper reports the first field observations of parental care in the Neotropical harvestman *Phareicranaus calcariferus* (Simon 1879) (Cranaidae) in Trinidad. Over the course of 25 days (9 July–3 August 2005), we made 12 observations of egg and early nymph guarding involving multiple juveniles and one or two adults (Table 1). In each case, we observed the adult and young only briefly (1–3 min) and then collected them. Adults and nymphs were preserved in the field in 10% formalin and later transferred to 70% ethanol for storage. Vouch-

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Table 1.—Young guarding in *Phareicranaus calcariferus* of Trinidad. Mount Tamana consists of a seasonal forest. Petite Tacarib is crappo-cocorite seasonal forest (disturbed rainforest). Morne Bleu Ridge is a montane rainforest. Palm sheath refers to the sheaths of palm fronds of *Euterpe broadwayii*.

Observation	Date	Location	Shelter	Number of young	Size of young	Adults present
1	9 Jul. 2005	Mount Tamana	log	≥ 25	larva	female
2	15 Jul. 2005	Petite Tacarib	log	4	late nymph	female
3	15 Jul. 2005	Petite Tacarib	log	≥ 25	larva	female
4	26 Jul. 2005	Morne Bleu Ridge	palm sheath	7	late nymph	female
5	26 Jul. 2005	Morne Bleu Ridge	palm sheath	17	early nymph	female
6	26 Jul. 2005	Morne Bleu Ridge	palm sheath	25	larva	female
7	26 Jul. 2005	Morne Bleu Ridge	palm sheath	25	larva	female
8	26 Jul. 2005	Morne Bleu Ridge	palm sheath	17	early nymph	female
9	26 Jul. 2005	Morne Bleu Ridge	palm sheath	20	early nymph	female
10	2 Aug. 2005	Morne Bleu Ridge	palm sheath	40	early nymph	female, male
11	3 Aug. 2005	Morne Bleu Ridge	palm sheath	4	late nymph	female, male
12	3 Aug. 2005	Morne Bleu Ridge	palm sheath	30	early nymph	female, male

er specimens were deposited into the natural history collections of the California Academy of Sciences, San Francisco (CAS) and Louisiana State Arthropod Museum, Baton Rouge (LSAM). In the field, adults were observed in close proximity to the nymphs, with their legs directly contacting those of one or more of the young. Nymphs and adults were collected from within or beneath a shelter (Table 1), either a rotting log or the sheath of a palm frond (*Euterpe broadwayi*). Our first observation occurred on 9 July 2005 on the slope of Mount Tamana (10°28'15.5"N, 61°11' 50.5"W; datum: WGS84) in the Central Range. The maximum elevation at this site is 325 m and the habitat that is present is a mixture of crappo-cocorite (jungle) and evergreen seasonal forest with a diverse assemblage of lianas and bromeliads (Murphy 1997). The second and third observations occurred on 15 July 2005 in the forests adjacent to the beach at Petite Tacarib (10°47'38.8"N, 61°13' 32.7"W; datum: WGS84) along the northern coast. At this location, the dominant habitat is disturbed rainforest (crappo-cocorite) and features several species of palms, bromeliads, and an understory dominated in many places by *Heliconia*. The remaining nine observations occurred from 26 July–3 August 2005 along Morne Bleu Ridge (10°43'59.3"N, 61°16'13.2"W; datum: WGS84) within 1 km of the summit of Mount Aipo in the Northern Range. The elevation of this area ranges from 700–840 m and the vegetation is characteristic of montane rainforest, featuring an abundance of lianas, bromeliads, palms and a relatively low canopy (6–12 m).

Nine of our observations involved the association of a single adult female and young (no male was observed or captured in the immediate vicinity of the shelter), while three instances involved both an adult female and male with early nymphs (Table 1).

We also made four observations from 26 July–2 August 2005 along Morne Bleu Ridge in which male and female harvestmen were found together, but there were no eggs or young present. In addition, an unguarded group of small young and a single unguarded clutch of eggs were found within the sheaths of palm fronds on 26 July 2005. We noted an inverse relationship between the number and the size of the young that were found. In general, the smallest instars (mean dorsal scute 2.1 mm, range 1.8–2.5 mm) also known as larvae (the first instar after hatching) were found in relatively large numbers (Table 1). Early (mean dorsal scute 3.6 mm, range 2.8–4.2 mm) and late nymphs (mean dorsal scute 5.2 mm, range 4.5–6.6 mm) were generally found in smaller numbers (Table 1). Our observations in the field were limited to generally 1–3 min because the adults and nymphs would disperse rapidly from the area once the shelter had been disturbed. Although we infer a guarding function for this behavior, we did not observe any instances of active defense of the young by the adults.

Our field study of *P. calcariferus* represents the first report of the reproductive biology for this species and is only the second observation of parental care for the Cranaidae and for harvestman in Trinidad (Machado & Warfel 2006). These observations indicate that this species exhibits maternal care and that guarding nymphs may involve both sexes. In two instances, we found unguarded eggs or juveniles. These observations may represent instances in which the guarding parent(s) had abandoned the brood, left in search of food, or were present but simply not found.

The inverse relationship between the number of nymphs present and body length of the juveniles indicates that the association between young and at least one of the parents may last for several weeks

or even months. We infer from the increases in body size that at least the first three instars of *P. calcariferus* may be guarded by at least one adult. This observed pattern also suggests that as the juveniles mature, they may either disperse or incur greater mortality due to predation.

We thank the Wildlife Section of the Forestry Division of the Ministry of Agriculture, Land, and Marine Resources of Trinidad and Tobago, W. I. for granting permission to conduct this research. We thank Paul Ressler, Mike Moore, and Stephen Broadbridge for assistance in the field, and G. Machado and an anonymous reviewer for critically reviewing the manuscript. This research was supported by grants from the Virginia Federation of Independent Colleges (RKH), Virginia Wesleyan College Faculty Summer Development Fund (VRT), and the Natural Science Undergraduate Research Fund at Virginia Wesleyan College. Specimens were legally collected and returned to the USA under export permit number 000541.

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Manuscript received 12 April 2006, revised 28 November 2006.

SHORT COMMUNICATION

MATERNAL OR PATERNAL EGG GUARDING? REVISITING PARENTAL CARE IN TRIAENONYCHID HARVESTMEN (OPILIONES)

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ABSTRACT. Based on a photo published in a book on New Zealand arachnids, I propose here that the cases of maternal care described by Forster in 1954 should be considered as paternal care. Maternal care is therefore restricted to the superfamily Gonyleptoidea, while paternal care has evolved in five phylogenetically independent lineages of Opiliones, including representatives of the superfamilies Travunioidea, Epedanoidea, and Gonyleptoidea.

Keywords: Evolution, *Karamea*, Laniatores, Soerensenellinae

In 1954, Ray Forster published a comprehensive study on New Zealand harvestmen in which he provided a detailed taxonomic account of the family Triaenonychidae and also described basic aspects of the natural history of some species. As far as I know, this work was the first record of maternal care in the order Opiliones. Based on field and laboratory observations, the author stated that all New Zealand representatives of the subfamily Soerensenellinae lay small groups of eggs ($n = 10\text{--}20$) on the undersurface of logs or rocks, which are guarded by the female. Some additional information is presented: “At intervals of a few days or a week further eggs are deposited so that in some cases egg masses of some 60–100 eggs may be found, some of which are hatching, while others are found at all stages, often including newly laid eggs” (Forster 1954).

There are several differences in the behavioral patterns of guarding females and guarding males in harvestmen, which are probably a consequence of the different selective pressures leading to the evolution of maternal care (via natural selection) or paternal care (probably via sexual selection). Perhaps the most striking difference is that females care for batches containing eggs in only one stage of embryonic development, while males care for batches containing eggs in several stages of embryonic development, likely from the result of different oviposition events (Machado et al. 2004). Therefore, the behavioral pattern of oviposition described for the New Zealand Soerensenellinae contrasts with all other harvestman species that present maternal care and is remarkably similar to the species that present

paternal care (see Machado et al. 2004). Unfortunately no photograph or drawings were provided in Forster’s paper and no voucher specimens were mentioned for the behavioral observations; thus it is not possible to examine the individuals studied by Forster in order to determine the identity of the sex that provides care.

More recently, Ray and Lynn Forster published a book called “Spiders of New Zealand and Their Worldwide Kin” (Forster & Forster 1999), which contains a brief description of the general biology of the New Zealand harvestmen, mostly based on the data previously presented in his paper of 1954. The book provides a color photo of an individual of *Karamea* sp. (Triaenonychidae, Soerensenellinae) guarding an egg-batch (Figure 1). This photo is highly informative since it clearly shows that the parental individual is a male and not a female. Many triaenonychid males are easily recognized due to the size of their swollen chelicerae and, in some species, also to the shape of the ocularium, which bends forwards while in females it is an erect spine (Lawrence 1937; Maury & Roig-Alsina 1985). Moreover, it is also possible to recognize in the photo that the eggs are in different stages of embryonic development (as described by Forster 1954), which is congruent with the multiple ovipositions observed in paternal harvestmen. Thus, Figure 1 provides unequivocal evidence that at least in this species of the genus *Karamea* the guarding individuals are males. However, there is no reason to believe that this case is an exception since Forster (1954) clearly states that all New Zealand Soerensenellinae show the same reproductive pattern.

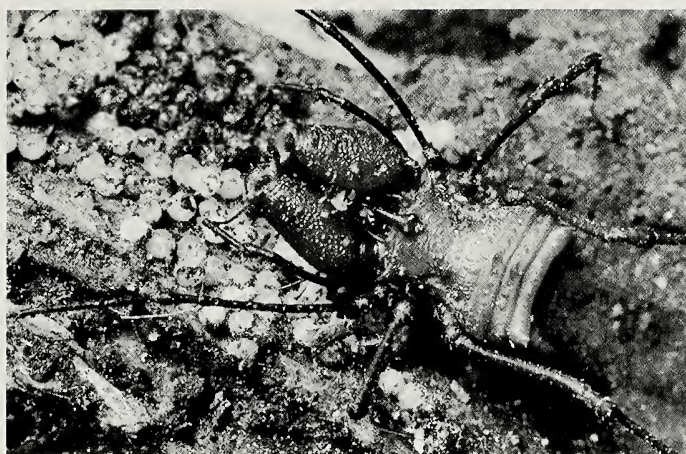


Figure 1.—Male of the triaenonychid harvestman *Karamea* sp. (Soerensenellinae) caring for eggs in different embryonic stages (noted by the difference in size and coloration) under a rotting log in New Zealand. Photo by Forster & Forster (1999), reproduced here with the permission of the University of Otago Press.

Consequently, paternal care, and not maternal care, is probably the rule in the subfamily. A final piece of information that can be extracted from the photo, which has never been mentioned by Forster, is that the debris is attached to the eggs, probably by the ovipositing females. This behavior has been previously described for several harvestman species of the families Cosmetidae and Gonyleptidae that present no care or exclusive maternal care (references in Willemart 2001), but it is the first record of its existence in a paternal species.

Debate about the existence of paternal care has been commonplace in the behavioral literature (see examples in Tallamy 2001), but misinterpretations about the sex of the guarding individuals are somewhat rare. Tallamy et al. (2004) recently showed that, with the assassin bug *Atopozelus pallens*, the females and not the males are responsible for egg protection. Curiously, like the case of triaenonychids reported here, the sexual dimorphism is quite evident and males and females can be easily recognized in the field. Another interesting case of mistaken parental identity is found in giant water bugs (Heteroptera: Belostomatidae) in which males of the subfamily Belostomatinae brood eggs laid by the females on their backs (Smith 1997). Since there is no clear sexual dimorphism among belostomatines, the parental behavior was originally attributed to females (Dimmock 1887). Surprisingly the mistake was not corrected for several years (Slater 1899), despite the fact that females are clearly unable to lay eggs on their own dorsum.

A putative explanation for Forster's mistake is that he was influenced by the widespread occurrence of maternal care in arthropods and the total absence of paternal care in arachnids until that moment. The first case of paternal assistance in the

arachnids was reported only at the end of the 1970s when Rodríguez & Guerrero (1976) described males of the manaosbiid harvestman *Zygopachylus albomarginis* Chamberlain 1925 guarding eggs and early hatched nymphs inside mud nests in Panama. Even if we take arthropods as a whole, the number of cases of paternal care in the literature by the 1950s was low (see references in Tallamy 2001). On the other hand, maternal care has been reported as early as the 18th and 19th centuries for non-social insects (e.g., Modeer 1764) and arachnids (e.g., Latreille 1802).

The presence of paternal care in the New Zealand triaenonychids has important implications for the evolution of the forms of parental care in the order Opiliones, particularly among the Laniatores. Maternal care is therefore restricted to the superfamily Gonyleptoidea, occurring in the families Cosmetidae, Cranidae, Gonyleptidae, and Stygnopsidae (see references in Machado & Raimundo 2001; Machado & Warfel 2006). The first real case of maternal assistance in harvestmen belongs to the gonyleptid *Acanthopachylus aculeatus* (Kirby 1818) from Uruguay (Capocasale & Bruno-Trezza 1964). Paternal care, on the other hand, has evolved in five phylogenetically independent lineages of Opiliones: once in Soerensenellinae triaenonychids (superfamily Travunioidea), once in podoctids (superfamily Epedanioidea), once in assamiids, and at least twice in gonyleptids (superfamily Gonyleptoidea) (see references in Machado et al. 2004).

I thank Wendy Harrex from the Otago University Press for giving me the permission to reproduce the photo of the male *Karamea*, Adriano B. Kury for identifying the sex of the individual in Figure 1, Rogelio Macías Ordóñez, Jeffrey W. Shultz, and two anonymous reviewers for comments on the

manuscript. GM is supported by grants from Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP, proc. #02/00381-0).

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Manuscript received 26 March 2006, revised 17 October 2006.

SHORT COMMUNICATION

ON A NEW SPECIES GROUP IN THE SPIDER GENUS *SOCALCHEMMIS* (ARANEAE, TENGELLIDAE)

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ABSTRACT. A new species, *Socalchemmis arroyoseco*, described from Monterey County, California, is clearly not a member of either of the species groups currently recognized in that genus, but does appear to be more closely related to those species groups than to the other genera in the *Liocranoides* complex.

Keywords: Taxonomy, North America, *Liocranoides*, *Anachemmis*, *Titiotus*, California

North America is home to a distinctive group of large hunting spiders with a remarkable character combination: the presence of three tarsal claws and claw tufts (tufts are usually found only in two-clawed taxa). This highly unusual combination of features has historically created difficulties both in the identification and phylogenetic placement of these taxa (Platnick 1999; Platnick & Ubick 2001, 2005). Four genera are currently recognized in this complex: *Liocranoides* Keyserling 1881 (in the eastern USA); and *Titiotus* Simon 1897, *Anachemmis* Chamberlin 1919, and *Socalchemmis* Platnick & Ubick 2001 (in California and adjacent states).

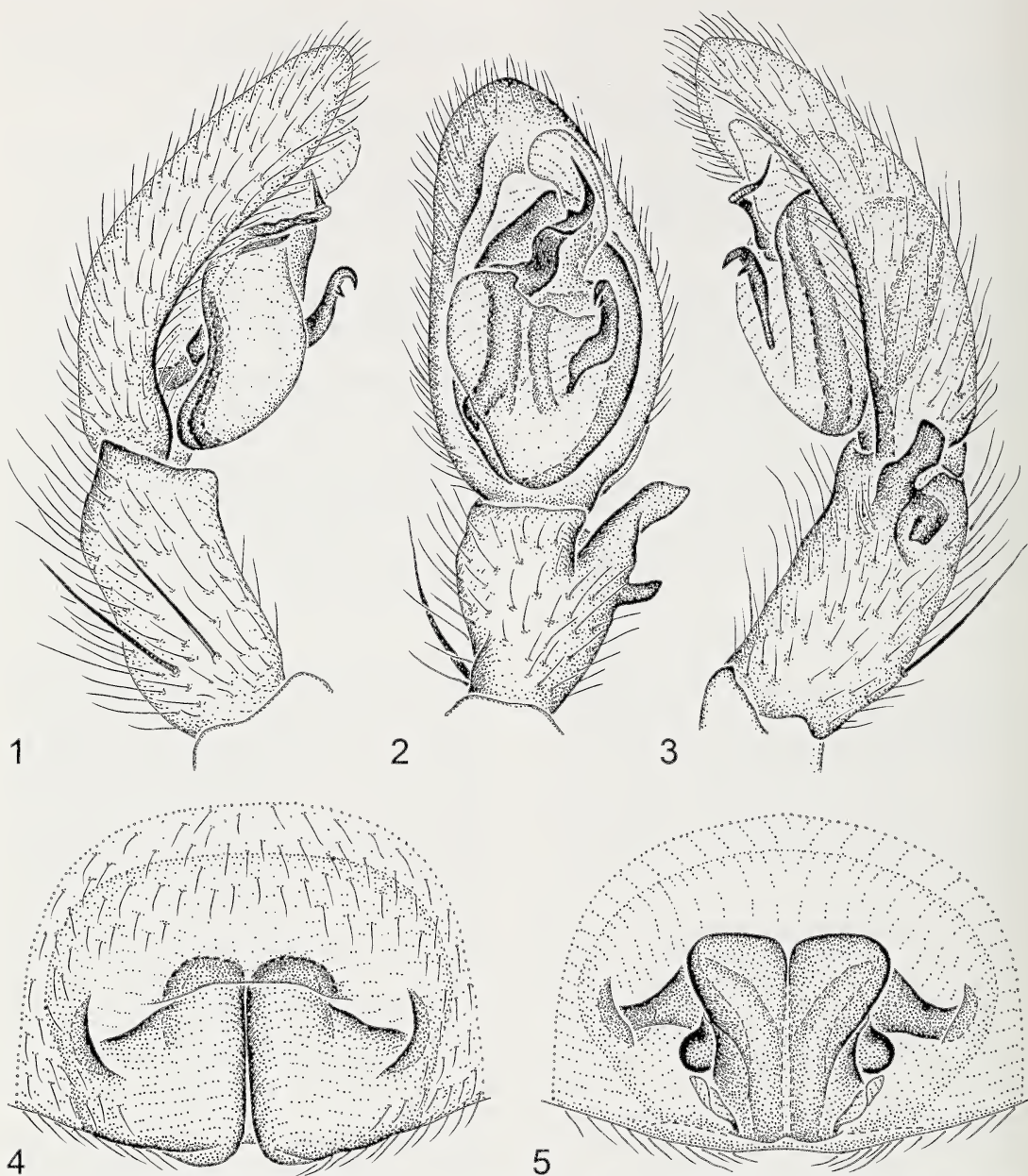
We report here on a remarkable new species recently collected in Monterey County, California, that clearly belongs to this complex but is not obviously a member of any of these four genera. It differs from the eastern species of *Liocranoides* in having an elongated median apophysis in males and lacking an elevated epigynal hood in females. It differs from the western genera as well. Males differ from those of *Titiotus* in having only two tibial apophyses, from those of *Anachemmis* in having the more dorsal tibial apophysis of males large and well-developed, and from those of *Socalchemmis* in lacking a prolateral extension at the base of the palpal embolus that results in a bipartite appearance of the embolus. Females differ from those of all three western genera in lacking a median epigynal septum.

The question, then, is what the closest relatives of the new species might be. No formal cladistic analysis of generic level relationships incorporating

all four genera has been conducted, and it isn't obvious that enough morphological characters are available to answer the question robustly. However, multiple features of the male palp suggest that the new species is more closely related to *Socalchemmis* than to the other three genera. The presence of an apical retrolateral tibial apophysis accompanied by a subapical, more dorsally situated apophysis suggests that the new species is closer to *Liocranoides* and *Socalchemmis* than to *Anachemmis* (males of which have only a tiny dorsal apophysis) or *Titiotus* (males of which have multiple apophyses, in a rather different conformation). In addition, both the embolus and the median apophysis are long and narrow (quite unlike the shorter and wider structures typical of *Liocranoides*, *Anachemmis*, and *Titiotus*).

Thus, we conclude that the new species is probably closest to *Socalchemmis*. Two species groups of *Socalchemmis* are currently recognized, but it is clear that the new species cannot be placed in either of those groups. Pending the discovery of additional taxa and a detailed cladistic analysis (hopefully including molecular data), we suggest that the new species probably represents the sister group of *Socalchemmis*, as currently constituted. Given the tentative nature of this conclusion, it seems better to expand the concept of *Socalchemmis*, at least temporarily, by including the new species as a third species group, rather than to create a new generic name that might prove, on further analysis, to be superfluous.

The new species is an outlier geographically, as



Figures 1–5.—*Socalchemmis arroyoseco* new species: 1. Left male palp, prolateral view; 2. Left male palp, ventral view; 3. Left male palp, retrolateral view; 4. Epigynum, ventral view; 5. Epigynum, dorsal view.

well; most *Socalchemmis* species occur in southern California and adjacent parts of Arizona and Baja California Norte. The new species is from the same area in Monterey County, California that is inhabited by the most northern of the previously known species, *S. monterey* Platnick and Ubick 2001. Specimens are deposited in the California Academy of Sciences, San Francisco (CAS) and the American Museum of Natural History, New York (AMNH).

Family Tenggellidae Dahl 1908

Genus *Socalchemmis* Platnick & Ubick 2001

Type species.—*Anachemmis dolichopus* Chamberlin 1919 by original designation.

Socalchemmis arroyoseco new species
Figs. 1–5

Material examined.—Holotype male and allotype female taken in pitfall traps in an oak forest at

an elevation of 1,126 ft [= 343 m] at Arroyo Seco, Indians Road, 36°13.8'N, 121°29.5'W, Monterey County, California, USA, 18 June–24 October 2004, D. & S. Ubick (CAS).

Other material examined: USA: *California*: Monterey County: 1 ♀, Indians Road, ca. 1 air km SSW Arroyo Seco Campground, 7 May 1995, oak forest, elev. 1,100 ft [= 335 m], D. Ubick, W. Savary (AMNH); 2 ♂, Arroyo Seco, Indians Road, 36°13.8'N, 121°29.5'W, 11 June–28 November 2003, pitfalls, oak forest, elev. 1,126 ft [= 343 m], D. & S. Ubick (AMNH); 1 ♂, same data, 18 June–24 October 2004, D. & S. Ubick (CAS); 2 ♂, Arroyo Seco, The Lakes, 36°13.9'N, 121°29.1'W, 19 August–11 November 2001, pitfalls, base of talus slope in oak-bay forest, elev. ca. 1000 ft [= 305 m], D. & S. Ubick (CAS).

Etymology.—The specific name is a noun in apposition taken from the type locality.

Diagnosis.—The sinuous, dentate embolus of males (Fig. 2), and the arched anterior epigynal margin of females (Fig. 4), are diagnostic.

Description.—*Male*: Total length 4.5 mm. Carapace pale yellow, darkest anteriorly; abdomen pale gray, unpatterned; femora yellow, more distal leg segments grading to light brown on metatarsi and tarsi. Leg spination typical for genus except: femora: I p0-1-1; II p0-2-1; III r2-1-1; IV r0-1-1; metatarsi: I p0-1-0, r0-1-0; II p1-1-0, r0-1-0. Embolus relatively long, twisted at about half its length, bearing distally directed denticle; dorsal tibial apophysis directed laterally, smaller than ventral apophysis (Figs. 1–3).

Female: Total length 4.9 mm. Coloration as in male. Leg spination typical for genus except: femora: I p0-1-1, r0-1-1; II p0-2-1, r1-1-1; III r0-2-1; IV r0-0-1; tibiae: I d0-0-0, p0-0-0, r0-0-0; II

d0-0-0; III r0-1-1; metatarsi: I, II p0-0-0, r0-0-0; IV p0-1-2, v3-3-1p. Epigynum without medium septum, with short lateral margins, distinct anterolateral margins, and arched anterior margin (Figs. 4, 5).

Natural history.—This species has been collected at three sites, two along Indians Road and the third just south of Arroyo Seco Campground, which enclose an area of only about 1 km in diameter. Although these sites are near the Hastings field station, extensive collecting there over several decades has produced no *Socalchemmis* specimens. All three of the inhabited sites are densely forested, primarily by oaks, but are adjacent to open canopy, formed by chaparral at Indians Road and an extensive talus slope at the campground site. The single specimen collected by hand was on the undersurface of a boulder deeply imbedded in porous soil. The specimens from pitfall traps suggest a surface activity in summer to autumn, whereas the hand-collected female was taken in early May.

Distribution.—Known only from the vicinity of Arroyo Seco in Monterey County, California.

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Manuscript received 3 May 2006, revised 1 August 2006.

SHORT COMMUNICATION

A NEW SPECIES OF *ERIGONOPLUS* (ARANEAE, LINYPHIIDAE) FROM CRIMEA, UKRAINE

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ABSTRACT. A new species of *Erigonoplus*, *E. galophilus*, is described from eastern Crimea, Ukraine.

Keywords: *Erigonoplus galophilus*, taxonomy, description

The linyphiid spider genus *Erigonoplus* Simon 1884 currently contains 19 species (Platnick 2004). The majority of these are rare and known only from single specimens (Dimitrov 2003; Eskov 1986; Eskov & Marusik 1997; Miller 1971; Millidge 1975; Millidge 1979; Tanasevitch 1989; Tanasevitch 1990; Thaler 1991; Wunderlich 1995). Species of *Erigonoplus* have been found in dry warm open places where they hide under stones or at the base of vegetation (Eskov 1986; Eskov & Marusik 1997; Miller 1971; Tanasevitch 1990; Thaler 1991; Wunderlich 1995). The distribution of the majority of *Erigonoplus* species is associated with the Ancient-Mediterranean region from Spain to Central Asia, with four exceptions: *E. globipes* (L. Koch 1872) has a Palearctic distribution; *E. justus* (O. P.-Cambridge 1875) occurs in Belgium; and *E. minaretifer* Eskov 1986 and *E. sibiricus* Eskov & Marusik 1997 occur in East and South Siberia. Recent collecting in eastern Crimea, Ukraine has revealed a new species of this genus, which is here described.

The materials examined for this study are deposited in the collection of Zoological Museum of Moscow State University (ZMMU), the Zoological Department of Sumy State Teacher's Training University (SSTTU) and in the author's private collection (VGC). The following abbreviations were utilized: E = embolus; Em = embolic membrane; M = membrane; P = paracymbium; Pt = protegulum; PTA = pedipalpal tibial apophysis; R = radix; St = subtegulum; T = tegulum; Tm = position of metatarsal trichobothria; TP = radical tailpiece.

TAXONOMY

Family Linyphiidae Blackwell 1859

Genus *Erigonoplus* Simon 1884

Type species.—*Erigone inclara* Simon 1881.

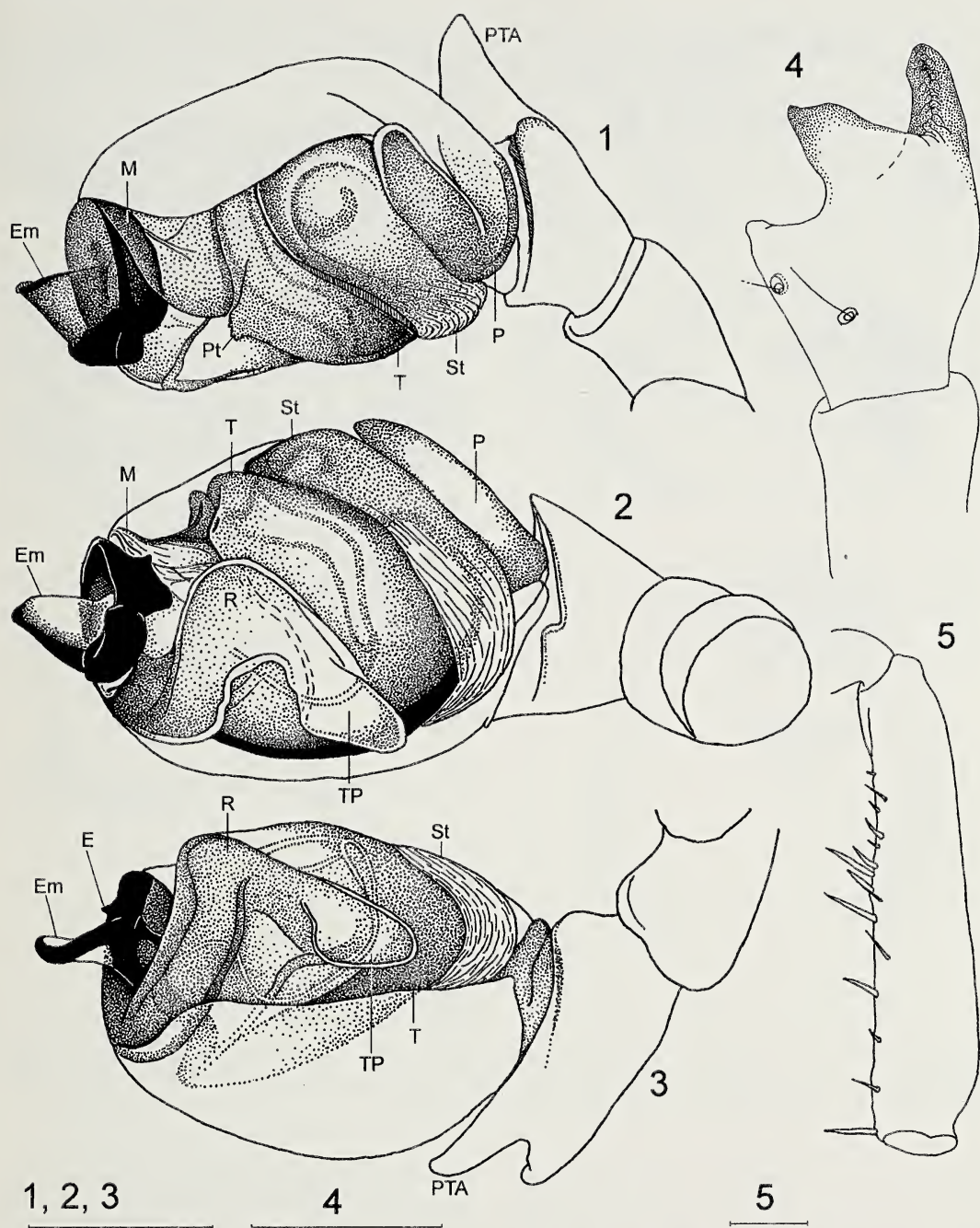
Remarks.—Species of *Erigonoplus* are generally small spiders with a total length of usually 1.2–1.8 mm, but one species (*E. simplex* Millidge 1979) is

2.45 mm; palpal tibia with 3 apophyses, dorso-lateral, dorsal, and lateral, the latter with a single trichobothrium. The embolic division has a strongly curved radix which has a large section turned aside from the body axis and which ends with a complex, strongly sclerotized distal piece. The male carapace varies from no elaboration or extension of the cephalic region [*E. inclarus* (Simon 1881), *E. inspinosus* Wunderlich 1995, *E. nobilis* Thaler 1991, *E. setosus* Wunderlich 1995 and *E. simplex*] to those forms with a strongly raised cephalic region [*E. castellanus* (O. P.-Cambridge 1875), *E. globipes*, *E. jarmilae* (Miller 1943), *E. justus*, *E. kirghizicus* Tanasevitch 1989, *E. minaretifer*, *E. nigrocaeruleus* (Simon 1881), *E. sibiricus* and *E. turriger* (Simon 1881)]. The male femur I either lacks setae (*E. inspinosus*) or bears a row of stout spines on its anterior surface. The tibial spinal formula varies from 0:0:0:0 (*E. minaretifer* and *E. sibiricus*) to 2:2:1:1 (*E. castellanus*, *E. inspinosus*, *E. simplex*) with the majority of species having a tibial spinal formula of 1:1:1:1. The abdomen of many species is coriaceous or has a poorly delimited scutum (*E. minaretifer*).

Erigonoplus galophilus new species Figs. 1–5, 8–11

Material examined.—Holotype male, allotype female, bank of Baracol salt lake, 12 km WSW of Pheodosia, eastern Crimea, Ukraine, 45°00'N, 32°14'E, 27 April 2003, V. Gnelitsa (ZMMU). Paratypes: 5 males, 4 females, same data (SSTU); 1 male, 1 female, same data (VGC); 1 female, same data except 16 October 2003 (VGC).

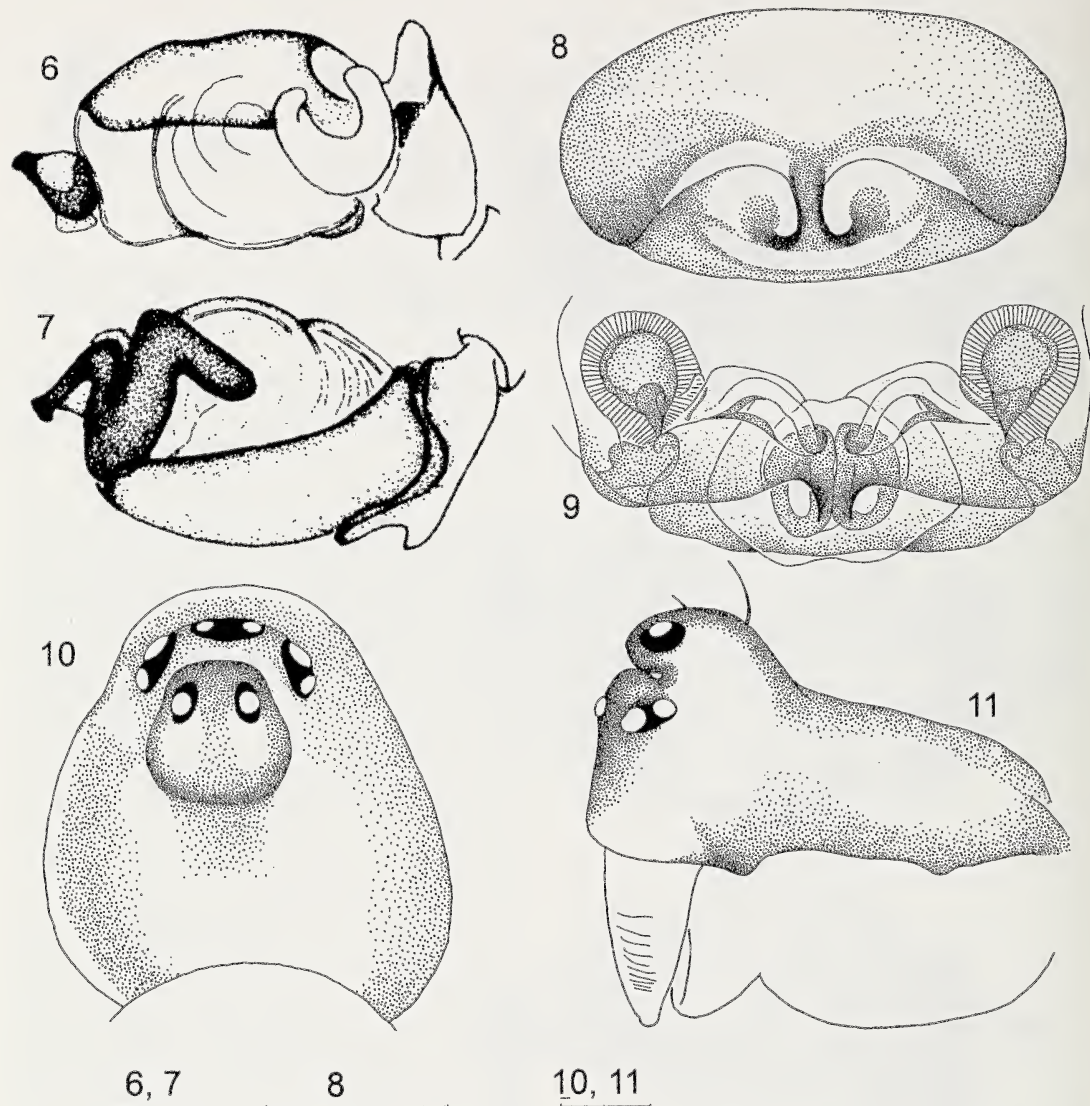
Diagnosis.—*Erigonoplus galophilus* appears to be most similar to *E. spinifemoralis* Dimitrov 2003 based upon the morphology of the palp (see Figs. 6, 7 for comparative figures). Males of *E. galophilus* differ from other *Erigonoplus* species by the tibial spine formula of 0:1:1:1; the stout ventral spines and their location on femur I; the shape of



Figures 1–5.—*Erigonopus galophilus* new species: 1. Left palp, ectal; 2. Left palp, ventral; 3. Left palp, mesal; 4. Left palpal tibia, dorsal; 5. Male femur I, lateral. Scale lines = 0.1 mm.

palpal tibia and the configuration of the palp particularly by the shape and proportions of radix and radical tailpiece as well as the form of distal part of embolic division. Females differ from other species of *Erigonopus* by the wide epigynum with narrow longitudinal partition reaching the center of the epigynum.

Description.—*Male*: Total length 1.47; carapace (Fig. 10, 11) yellow-gray; length 0.62; width 0.53; sternum: length 0.40; width 0.38; covered with scattered long thin setae; eyes: width between the posterior median eyes is twice the PME diameter. Leg lengths: leg I: femur 0.52, patella 0.17, tibia 0.43, metatarsus 0.42, tarsus 0.29; leg II: femur 0.48, pa-



Figures 6–11.—6, 7. *Erigonoplus spinifemoralis* (from Dimitrov 2003): 6. Right palp, ectal; 7. Right palp, mesal. 8–11. *Erigonoplus galophilus* new species: 8. Epigynum, ventral; 9. Vulva; 10. Male carapace, lateral; 11. Male carapace, dorsal. Scale lines = 0.1 mm.

tella 0.17, tibia 0.38, metatarsus 0.42, tarsus 0.27; leg III: femur 0.43, patella 0.15, tibia 0.31, metatarsus 0.32, tarsus –; leg IV: femur 0.59, patella 0.18, tibia 0.50, metatarsus 0.48, tarsus 0.29; femur I ventrally with strong setae (Fig. 5); tibial spines 0:1:1:1; TmI 0.45; TmIV absent. Abdomen: black with two brown chitinous sigillae; covered with long setae. Palp (Figs. 1–3): radix with large tail-piece and massive heavy sclerotized curved distal part, embolus short and barely visible, a wide embolic membrane with strongly sclerotized outer margin; palpal tibia (Fig. 4) with 3 apophyses.

Female: Total length 1.61; carapace dark brown, length 0.59; width 0.53; sternum: length 1.32; width

1.10; dark brown; eyes: posterior median eyes are one diameter PME apart. Legs: leg I: femur 0.50, patella 0.17, tibia 0.42, metatarsus 0.36, tarsus 0.27; leg II: femur 0.45, patella 0.17, tibia 0.36, metatarsus 0.34, tarsus 0.27; leg III: femur 0.41, patella 0.17, tibia 0.30, metatarsus 0.31, tarsus 0.24; leg IV: femur 0.59, patella 0.17, tibia 0.48, metatarsus 0.42, tarsus 0.28; tibial spines 1:1:1:1; TmI 0.46; TmIV absent. Abdomen: black without chitinous sigillae. Epigynum (Fig. 8) 3.5 times broader than long, narrow central part with parallel margins curved aside in the hind pieces nearly at the center of epigynum, vulva (Fig. 9).

Ecology.—The specimens were all collected us-

ing a hand-held suction sampler in detritus and on the soil within the strip of *Salicornia* on the banks of the salt lake.

I would like to thank Dr Christo Deltshev (Sofia, Bulgaria) for making some important comments on a version of the manuscript.

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Manuscript received 29 November 2004, revised 12 June 2005.

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Figures 1–4. *A-us x-us*, male from Timbuktu. 1, Left leg; 2, Right chelicera; 3, Dorsal aspect of genitalia; 4, Ventral aspect of abdomen. Scale = 1.0 mm.

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SHORT COMMUNICATIONS

Short Communications are usually limited to three journal pages, including tables and figures. The format is open, but internal headings (Methods, Results, etc.) are omitted. They are printed in a smaller (10 point) typeface. An Abstract is required.



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